

EXPERIMENTAL ANALYSIS OF BEHAVIORAL ISOLATION AMONG
FOUR SIBLING SPECIES OF NEMOBIINE CRICKETS

By

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To Esther

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Abstract of Dissertation Presented to the Graduate Council
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EXPERIMENTAL ANALYSIS OF BEHAVIORAL ISOLATION AMONG
FOUR SILLING SPECIES OF NEBOBIINE CRICKETS

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Picrodactylus debilis (Scudder)," formerly considered a single species, is four closely related species, separable by male song, color pattern, intersterility, and female phoresis. These species occur sympatrically and yet are separated by the closest series of species specific calling song pulse rates known for any complex of sympatric cricket species: approximately 37, 47, 55 and 60 p/s at 25°C. The geographic and ecological ranges of the four species are delineated from more than 700 laboratory recordings of crickets from more than 100 localities. The 37 p/s and 55 p/s species overlap broadly through much of the xeric sand ridge of Florida. The 55 p/s species often occurs in the central ridge scrub association and in the east and west coastal dunes. The 37 p/s species ranges northward into the upland longleaf-pine and turkey-oak where the 55 p/s species is absent. The 47 p/s species (the real ambitosus) occurs in pastures, roadsides, and

disturbed xeric and mesic bar oaks. The 60 p/s species, occasionally intermixed with the 47 p/s species, lives in the pine flatwoods from east Gainesville to the Okefenokee Swamp of Georgia. Populations morphologically similar to the 60 p/s species, but with pulse rates of 50-51, occur from Lafayette and Taylor Counties west into the Florida panhandle sometimes in association with the 37 p/s species. Of 14 intraspecific allopatric crosses between distant populations, all mated normally and 11 produced progeny. The range of pulse rates from intraspecific allopatric populations throughout central Florida exceeds the interspecific differences that occur between closely related species pairs in areas of sympatry. Interspecific pulse rate overlap in areas of sympatry appeared likely on cold clear days because temperatures where these crickets lived ranged from 15-20°C in the shade to 30-35°C in the sun. Individual temperature determinations derived from 71 field-recorded male calling songs suggested that males locate in microhabitats which maintain and probably enhance differences between closely related species pairs. The identity and exact location of 1624 male Pictonemobius from 51 separate hourly sampling periods on a one-acre plot defined male calling song production as diurnal and bimodal with a distinct morning and late afternoon peak. Pictonemobius spp. are present in all stages throughout the year, even where Weather Service temperatures below -8°C occur yearly;

however, eggs, nymphs and adults were killed by a controlled, simulated natural temperature regime of -8°C . Synthetic signals, controlled in carrier frequency (7,000Hz), sound level (75 db), pulse rate (varied with test), pulse duration, chirp length and interval, and pulse shape were used to test females in the laboratory. Females of each species, when presented with replicated series of seven randomly ordered, synthetic trills differing by 2.2 p/s responded to pulse rates corresponding to calling songs of their conspecific males. Both visual scoring and a motion detector coupled to an event recorder revealed the same peaks of female response. Sixty-four virgin females, 16 of each species, were tested to determine the extent of reproductive isolation under conditions of forced crossing. Females were pretreated for responsiveness 24 hours prior to a 4-hour mating observation period. In 16 control pairings the mating sequence proceeded normally. In 48 heterospecific crosses 26 produced calling song; 12 courtship song; 10 the first, spermatophoreless mounting; 9 a spermatophore and an attempt at mounting; 4 a spermatophore transfer and its retention by the female for more than 5 minutes; and 1 hybrid progeny with a pulse rate intermediate between the parental types. Approximately 90% of pinned specimens examined can be identified using a combination of locality, color pattern and stridulatory file characteristics.

INTRODUCTION

Among the most common diurnal singing Orthoptera throughout most of peninsular Florida and somewhat northward are the nerobiine ground crickets now known as Pictonemobius ambitiosus (Scudder). Both sexes are flightless, possessing only forewings; in the case of the female these tegmina are somewhat reduced, exposing the last abdominal segments. The male's tegmina are usually dark with light borders giving him a trim, waist-coated appearance. Both sexes have a prominent white bar on the front of their head between the eyes. In a letter to Dr. T. J. Walker dated 23 September 1964, T. H. Holbell noted that he had found differences in morphology and coloration between Florida populations of ambitiosus from different ecological situations. At that time Walker had noted differences in calling song pulse rate between collections made in moist low areas and well-drained sandhill areas. In a temperature vs. wingstroke study (Walker, 1962), one individual cricket maintained a wing stroke rate approximately 6-8 pulses/second (p/s) less than the others over the range of temperatures tested, and was designated as "slow" ambitiosus while the remaining were termed "fast" ambitiosus.

Additional specimens of "slow" ambitiosus were collected by John D. Spooner in an area known as the Gainesville

Gun Club, near the municipal airport. "Slow" P. ambitiosus, with a calling song pulse rate of 37 p/s at 25°C, was given a University of Florida Department of Entomology tape library specimen recording code number of 528. "Fast" P. ambitiosus, with a pulse rate of 47 p/s at 25°C was given code number 531. These two types of crickets could be distinguished at the municipal airport. Crickets producing 528 songs were most commonly found in the disturbed and weedy turkey-oak areas whereas crickets producing 531 songs were found in the surrounding hammock. In another locality (Goldhead Branch State Park, Clay Co.) both 528 and 531 crickets were again collected in close association.

Field collected adult females taken to the laboratory and isolated in gallon jars provisioned with food and water and approximately 2 inches of autoclaved and sifted sand, soon produced progeny that were either 100% 528 or 100% 531. Generally the 528 females were more black and white speckled above and white below, while the 531 were marked in softer tones of brown and tan with tan venters. The nymphs of the two types were distinctively and consistently marked and colored allowing about 90% accuracy in separating them. The number of teeth and the length of the sound producing wing file varied between 528 and 531. These data suggested that 528 and 531 were two species based on behavioral and morphological grounds despite overlap in habitat, and the presence of some individuals with intermediate color patterns.

In a turkey-oak, sandhill area 3/4 mi. west of Archer, Florida, on 5 April 1967, I discovered females of Pictonemobius that were dark brown with bright straw colored markings as well as the more typical dull-brown females of Pictonemobius 531. Their differences were quite striking. One individual female of each color type was brought to the laboratory and each gave rise to progeny which were true and bred true to their parental color type. Laboratory tape recordings of the resulting male progeny fell into two categories corresponding with the two parental female color types. The dull-brown type, known from many other localities in Florida, (previously designated as 531) had a calling song pulse rate of 47 p/s at 25°C. The new, dark-brown, brightly marked P. ambitiosus had a calling song of approximately 55 p/s at 25°C.

Recordings of field-collected P. ambitiosus from the Archer locality confirmed the new male song type in the field. Numerous recordings had already been made under the 531 number for the two types, so the notation 531-D for the Dull brown (47 p/s) and 531-B for the Brightly marked (55 p/s) P. ambitiosus was instituted.

Type 531-B was found to breed true wherever it was found and could be separated from 531-D and 528 in central Florida by pulse rate and color pattern 100% of the time. Some individual 531-B had stridulatory files that were within the range of stridulatory file lengths of 528 or

531-D, making this character less dependable in terms of separating species. Type 531-B appeared to be distinct from 531-D and 528.

A fourth P. ambitiosus song type was discovered by the author on 25 February 1969 along a grassy roadside and in the surrounding pine flatwoods, .3 mi. east of the Clay Co. line on Florida road S 16. The male calling song attracted my attention because it resembled that of Miogryllus saussurei (Scudder) (which was singing from burrows at the same time) but differed from M. saussurei by having chirps lasting more than 2 seconds. A 531-D male was located at the same site by its calling song and provided a contrasting reference to this new song type, designated as Pictonemobius sp. 525. The calling song pulse rate was about 60 p/s at 25°C. Both males and females were darkly marked, and easily distinguishable from the other three types.

Early in this study the four song types appeared to represent biological entities, possessing characteristics of species with regard to reproductive isolation and ecological and geographical distribution. I will refer to them as species 528, 531-D, 531-B and 525 from this point and will present proof of their separateness in the remaining sections of this paper.

SONG ANALYSIS

Equipment: Recording and Analysis

Tape recordings of male crickets were made in the Department of Entomology low noise room (LNR).¹ The crickets were caged individually in 4 x 4 x 4 in. screen-sided cages. Caged singers were located by using an ear-phone monitor, and recorded with a dynamic microphone on Scotch 202 magnetic recording tape at 15 inches/sec. on an Ampex model 351 tape recorder. The tape recorder was located in an adjoining laboratory and was activated by remote controls from within the LNR. Some tape recorded sounds were analyzed with a Kay Electric Company audio-spectrograph (Sona-Graph) but calibration procedures were lengthy and production was slow. More often I used an oscilloscope with a "storage screen." Several different complete chirps could be displayed at one time on the oscilloscope using a sweep rate of .05 sec/cm. From a total of 30 pulses the pulse rate was determined by the formula

$$p/s = \frac{30}{.05D}$$

¹The mean A-weighted sound pressure level (SPL) was below 30 dB (re. 0.0002 dynes/cm²) as determined by a General Radio Model 1551-B sound level meter.

where D = mm required for a 30 pulse display and .05 is the sweep rate (.05 sec/cm).

Calling song pulse rates are a function of the temperature of the individual cricket and therefore can be corrected to some temperature standard for comparative purposes given the slope of the pulse-rate-vs.-temperature plot. Pulse rate corrections to 25°C were made with the formula

$$p/s \text{ at } 25.0^{\circ}\text{C} = (25.0^{\circ} - T) 2.232 + p/s \text{ at } T$$

where T = temperature at time of recording and 2.232 = slope of the pulse-rate-vs.-temperature plot (Walker 1962).

Description of Calling Songs

The calling songs of Pictonemobius, like the calling songs of other Gryllidae, are produced by solitary adult males and attract sexually responsive females. Such songs have been shown to be species specific with respect to the females that are attracted (Walker 1957, Alexander 1967, Hill et al. 1972, Ulagaraj 1974).

On numerous occasions two or more of the four Pictonemobius species have been heard calling in the same area. In such areas individuals with intermediate songs have not been found.

Crickets of the genus Pictonemobius are chirping crickets, i.e. males produce short (<5 sec.) series of

pulses of sound ("chirps") as opposed to trilling crickets which produce long (>5 sec.) series of pulses ("trills"). Each pulse is created by a single closure of the upheld mesothoracic wings, during which the file (ventral, right wing) is in contact with the scraper (dorsal, left wing). The pulses are discrete bursts of sound having fundamental oscillations in the 5,000-7,000 Hz range. These fundamental oscillations correspond with strikes of file teeth on the scraper.

Species 528 has a long chirp, approximately 1-2 sec. in duration, with a pulse rate of 36.7 p/s at 25°C (n=21), municipal airport, Gainesville, Florida. Oscillographic traces of a 528 calling song are in Fig. 1A. The long chirp makes the pulse rate sound even slower to the human listener, compared with 531-D.

Species 531-D has a chirp of intermediate length, 0.3 to 0.8 sec., with a pulse rate of 47.0 p/s at 25°C (n=9) from the municipal airport, Gainesville, Florida. A complete chirp, 20 pulses long, and a series of regularly spaced chirps are shown in Fig. 1B.

Species 531-B has a short chirp, less than 0.5 sec. in length, with a pulse rate of 54.9 at 25°C (n=21) from 3/4 mi. west of Archer, Florida. Some individuals consistently produce 9 and 10 pulse chirps while others produce chirps up to 20 pulses long, overlapping in chirp length with 531-D. A typical series of 7 chirps, and one 14 pulsed chirp are shown in Fig. 1C.

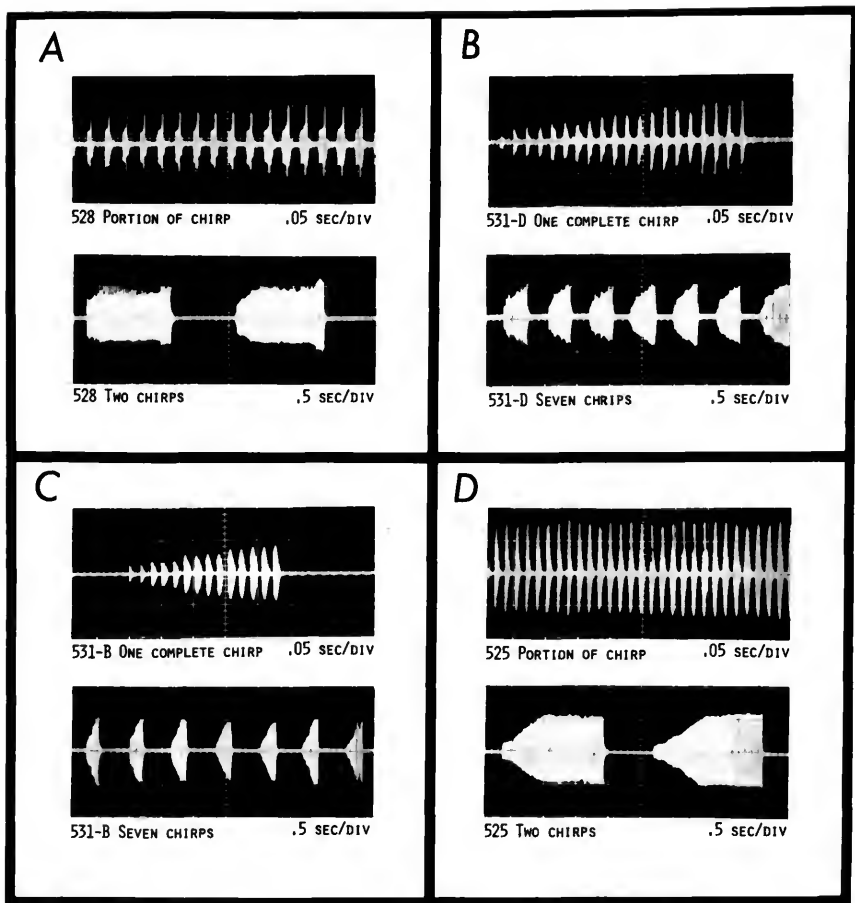


Fig. 1. Calling songs of 4 species of *Pictonemobius* at 25.0 to 26.3°C. A. 528, municipal airport, Gainesville, Florida, 25 Jan. 1967 (U. F. Tape No. 528-54). B. 531-D, municipal airport, Gainesville, Florida, 19 Oct. 1966 (531-60). C. 531-B, 3/4 mi. west Archer, 4 June 1969 (531-218). D. 525, .2 mi. east on S400A, 3.0 mi. north Orange Hts., 29 May 1969 (525-9).

Species 525 has a long chirp, as long or longer than 528, usually 1-2 sec. long, and the fastest Pictonemobius pulse rate, 59.9 p/s at 25°C (n=8) at .3 mi. east of the Clay Co. line on SR16. The trend of decreasing pulse rate with increase in chirp length from 531-B to 528 makes the 525 song quite unusual to hear. Adding to its distinctness is a slow build-up in intensity in the early part of the chirp (Fig. 1D).

For all Pictonemobius songs individual variation exists in the number of chirps per unit time, the intensity changes within the chirp, and the maximum intensity of the chirp. These differences remain consistent throughout a sample of an individual's calling song. Several laboratory-reared 528 and 531-D were found to have irregularly spaced pulses within a chirp if recorded shortly after their maturation to the adult stage. No field-collected or laboratory-reared specimens more than one week old were found to be irregular in this manner. The geographic distribution and compilation of the calling song pulse rates presented later in this section will serve to define the four species of Pictonemobius.

Description of Courtship Songs

The acoustical signals associated with mating are described and illustrated here to supplement my earlier (Mays 1971) paper on the mating behavior of Pictonemobius. The pattern of courtship sound production is similar for the four species 528, 531-D, 531-B and 525.

The principal courtship song (with or without a spermatophore) is characteristically a long series of soft chirps (often irregularly spaced) in which the first 5-10 pulses are produced at almost exactly $1/2$ the calling song pulse rate, followed by resumption of the typical rate, and an increase in intensity (Fig. 2, B & D).

When a male loses contact with the female he is courting he often produces a loud and extended pulsed chirp (Fig. 2C) usually beginning with courtship-type wide-spaced pulses. Prior to "backing under" for both the "brief spermatophoreless mounting" and the "lengthy mounting and [spermatophore] transfer" (Mays 1971) a long trill is produced, entirely at the calling song pulse rate (Fig. 2E).

Courtship chirps for 528 and 525 are shorter than calling song chirps. Courtship interruption chirps and backing under trills for 531-D and 531-B are much longer than their calling song chirps. The untrained listener would likely find it difficult to distinguish among the courtship chirps of the four species but easy to distinguish courtship chirps from calling chirps.

Geographic Distribution

Crickets belonging to the genus Pictonemobius occur principally in Florida and in the immediately adjoining portions of Georgia and Alabama. T. J. Walker has field recordings from Decatur, Brooks, and Cobb Co., Georgia, and

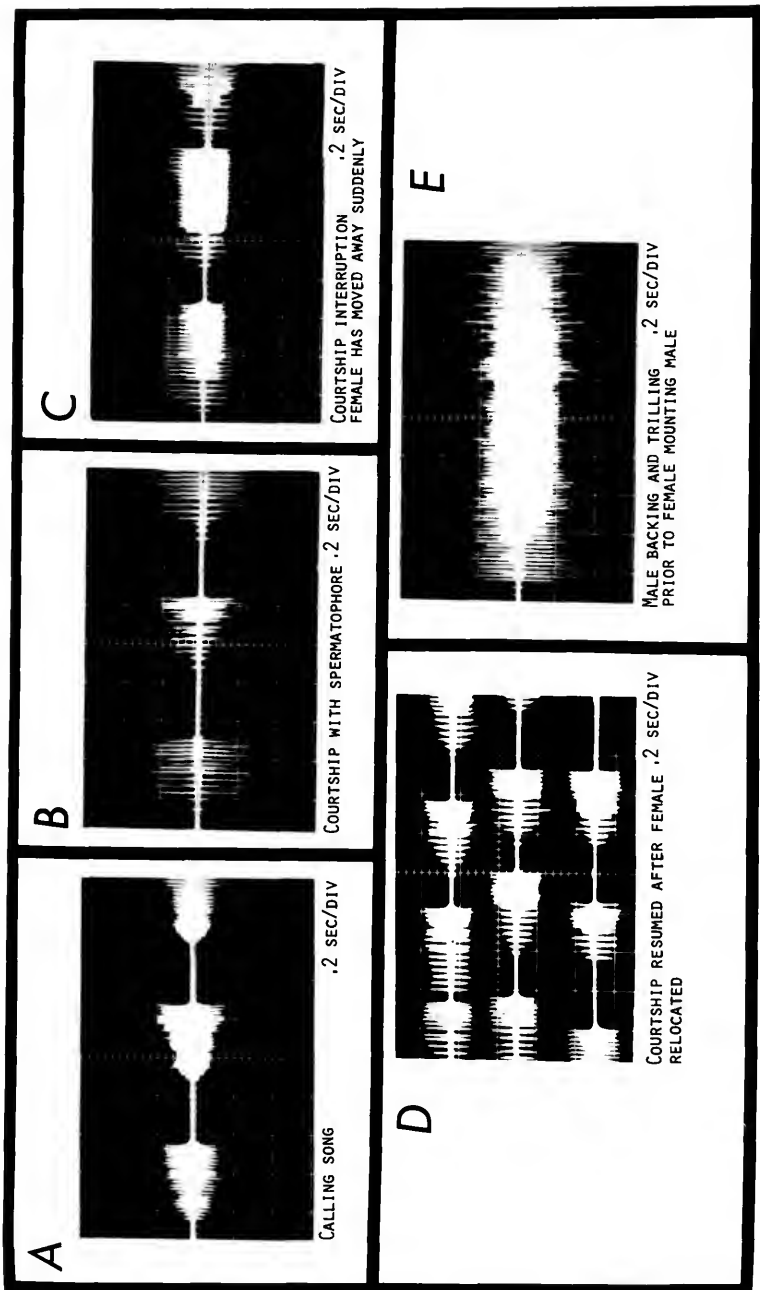


Fig. 2. Acoustical repertoire of *Pictonemobius* 531-D male in laboratory at $25.5 \pm .5^{\circ}\text{C}$. A. Municipal airport, Gainesville, Florida, 19 Oct. 1966 (531-60). B-E. Montecocha Rd., 10 mi. north of Gainesville, 24 Feb. 1968 (531-166).

Cleburne Co., Alabama. I have been unsuccessful in locating Pictonemobius west of the Florida panhandle, and north of southern Alabama and central Georgia.

Collections and laboratory tape recordings of more than 700 Pictonemobius from over 100 Florida localities fall into the four categories of Pictonemobius discovered in the Alachua Co. area. The identity of field-collected specimens was determined by analysis of laboratory recordings of male calling songs, habitat specificity, and color patterns.

The areas of distribution overlap do not necessarily indicate intimate sympatry. Localities in which such sympatry was in evidence are listed (Table 1) and illustrated (Figs. 3, 4, 5, & 6).

The analysis of calling songs from several areas of sympatry defined the species numerous times. Marler (1962) states "Judgments of degrees of species specificity are relative and arise from comparisons between signals under consideration and other signals which are likely to be present at the same time and place" (p. 538). After several areas of sympatry were understood, widely separated populations of each of the four kinds could be related over a wide geographic area including most of Florida. A detailed analysis of allopatric variation in Pictonemobius is not presented here, and would not necessarily serve to further define the species already recognized. A discussion of inconsistencies in 525 from the Panhandle region (Table 1) is in the Appendix.

Table 1. Locality and pulse rate information* on 4 species of Pictomicrobius.

Locality number	528			531-D			531-B			525		
	n	\bar{P}/s	SD	n	\bar{P}/s	SD	n	\bar{P}/s	SD	n	\bar{P}/s	SD
		at 25°C			at 25°C			at 25°C			at 25°C	
		Range		Range			Range			Range		Range
1	21	36.7	1.2	34-38	9	47.0	1.1	46-49				
2	11	35.9	1.4	34-39	20	45.8	1.4	44-47				
3	5	33.1	1.7	30-35	13	46.7	1.4	44-49		**		
4	2	38.0	.9	37-39								
5	1	35.1			9	47.2	1.7	45-50	21	54.9	1.4	53-57
6					**					5	60.4	2.3
7	8	35.7	1.2	34-37								
8										1	49.8	
9	10	41.0		40-43								
10					**					8	59.9	1.9
11												56-62
12												
13	2	37.2	1.3	36-38								
14	2	38.9	.7	38-39								
15	2	35.9	4.6	33-39								

Table 1 - continued

Locality number	528 p/s at 25°C			531-D p/s at 25°C			531-B p/s at 25°C			525 p/s at 25°C		
	n	\bar{X}	SD	n	\bar{X}	SD	n	\bar{X}	SD	n	\bar{X}	SD
16				9	43.7	1.7	42-27					
17	1	34.7					11	46.6	1.7	44-49		
18							1	51.8				
19							3	55.7	5.9	52-62 ^{††}		
20										1 [†]	48.8	
21										1 [†]	54.1	
22												
23	3	34.6	1.6	33-36	4	48.7	1.0	47-49				
24					7	47.3	1.0	46-49				
25					1	47.0						
26	**				14	46.4	1.8	44-50				
27	1	35.5			7	46.3	.8	45-47	2	51.6	1.4	51-53
28	2	38.0	.4	38					2	53.8	.6	53-54
29	33	38.3	.9	36-40	1	45.3			3	55.4	1.8	54-57
30	1	36.4							3	52.9	.5	52-53

Notes to Table 1Alachua Co.

1. Municipal airport, Gainesville (NE. 1/4 of Sec. 24, R.20E., T.9S.) "Gun Club" (T.J. Walker collections)
2. Montecocha Rd. 10 mi. north of Gainesville, east of Fairbanks
3. Gainesville & vicinity: several inc. N. 39th Ave. and NE. 15th St.; S.W. Archer Rd., 3700 block; Millhopper; Division of Plant Industry Bldg., U. of F. campus
4. Alachua-Levy Co. line & SR.24
5. 3/4 mi. west of Archer, south of SR.24
6. .2 mi. east on S200A from jct. with US.301

Baker Co.

7. .1 mi. south of Georgia state line on SR.121
.2 mi. west on S23B from SR.121

Bay Co.

8. Panama City Beach, NE. city limits, east of Highland Dr.

Clay Co.

9. Goldhead Branch State Park (T. J. Walker collections)
10. .3 mi. east of Clay Co. line on SR.16 & vicinity of Starke Country Club

Collier Co.

11. 1/2 mi. south of jct. 840 & 29 & jct. 840 & 29
12. 2 mi. south of 865 on 865A, near beach

Columbia Co.

13. 3.0 mi. south of Suwannee Co. line off US. 27

Flagler Co.

14. South of Marineland

Franklin Co.

15. Carrabelle, nr. cemetery, north side of town

Gilchrist Co.

16. Jenny Springs

Hernando Co.

17. 2 mi. south of Croom west of I-75

Highlands Co.

18. Archbold Biological Station

19. Venus

Jefferson Co.

20. .5 mi. north US.96 on SR.59

LaFayette Co.

21. 4.0 mi. north of Dixie Co. line, S357

Lake Co.

22. Leesburg city limits, south on US.27

Leon Co.

23. Tall Timbers Research Station, north of Lake Lamonia

Levy Co.

24. 1.9 mi. west of Otter Creek, then 4.5 mi. north

25. 1 mi. north Bronson, flatwoods

26. 1.5 mi. north Marion-Levy Co. line on US.41

27. Manatee Springs

28. Near Shell Mound, S326 north of Cedar Key

29. .5 mi. east, .5 mi. north of Bronson

Macon Co.

- 30. .7 mi. north of Sparr on "old" 301
- 31. Ocala, east city limits
- 32. SR.40 & S336
- 33. US.27 & 441 at Orangeblossom Hills
- 34. S484 at Dunellon
- 35. Nr. jct. S200 & S484; 5 mi. east jct. S200 & S484

Palm Beach Co.

- 36. Jupiter

Putnam Co.

- 37. 2 mi. east Melrose

Seminole Co.

- 38. Sanford, nr. E. 25th St. and Grandview, 1/2 mi. northwest of "Fort Reed"

Sumter Co.

- 39. Sumter-Lake Co. line & SR.50

Taylor Co.

- 40. Blue Springs 1 mi. north of Cedar Island
- 41. Forest Capital State Park
- 42. 5 mi. south of Perry

Wakulla Co.

- 43. 1/2 mi. west of jct. SR.365 on SR.98

GeorgiaClinch Co.

- 44. Mile post #7 on Ga.177

Brooks Co.

45. Quitman

Decatur Co.

46. West of Climax

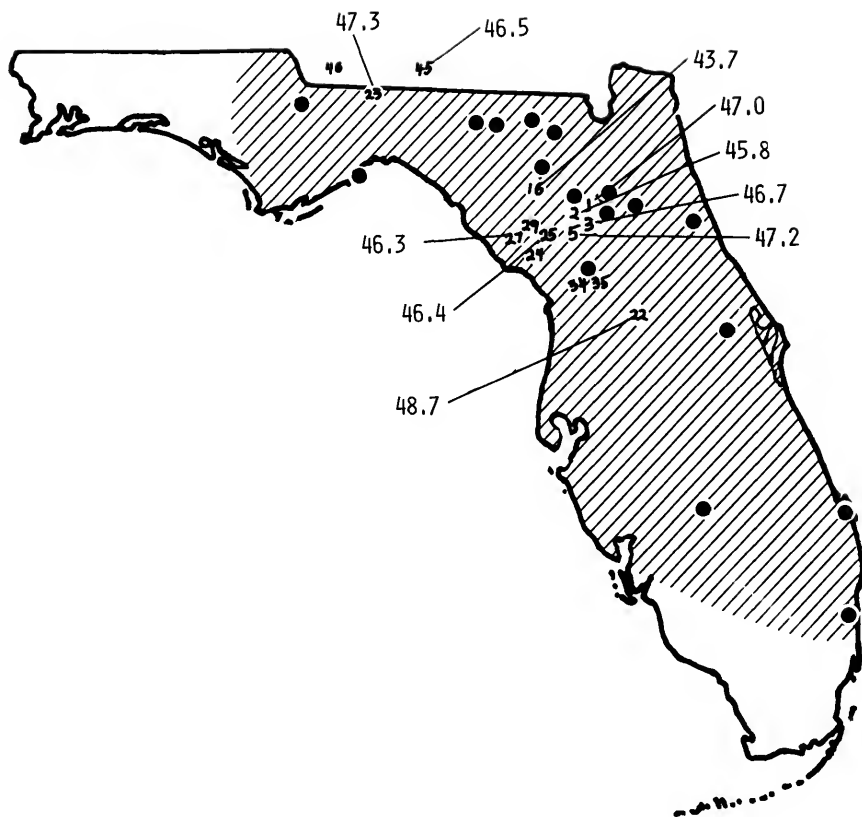


Fig. 4. Distribution of *Pictonemobius* sp. 531-D in Florida. Hand printed locality numbers refer to numbered sites in Table 1. Additional localities are indicated by unnumbered dots. Mean pulse rates for localities with 3 or more individuals assayed (Table 1) are to the left and right of the Florida peninsula.

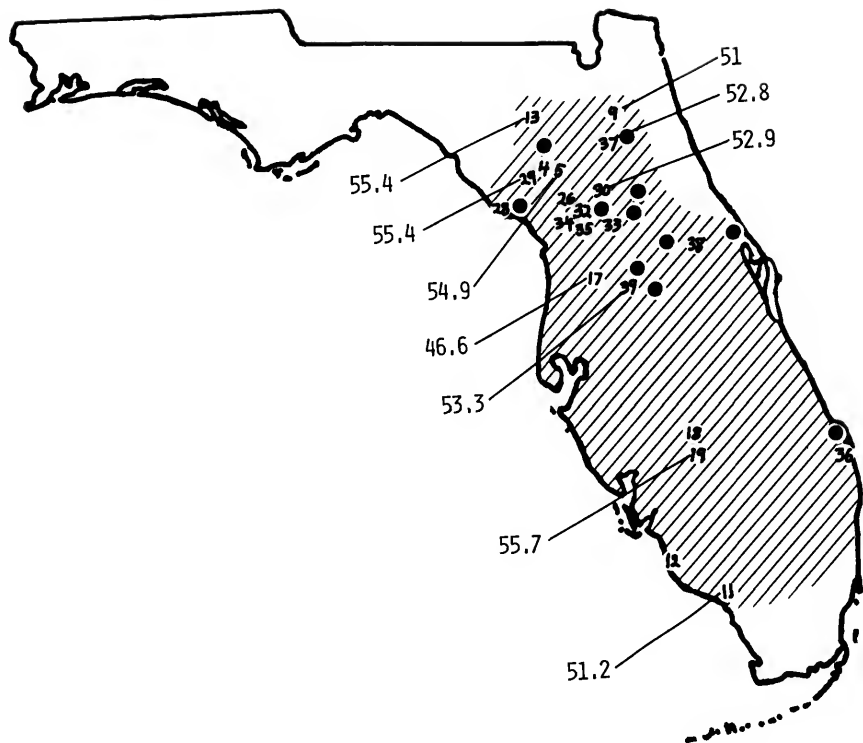


Fig. 5. Distribution of *Pictonemobius* sp. 531-B in Florida. Hand printed locality numbers refer to numbered sites in Table 1. Additional localities are indicated by unnumbered dots. Mean pulse rates for localities with 3 or more individuals assayed (Table 1) are to the left and right of the Florida peninsula.

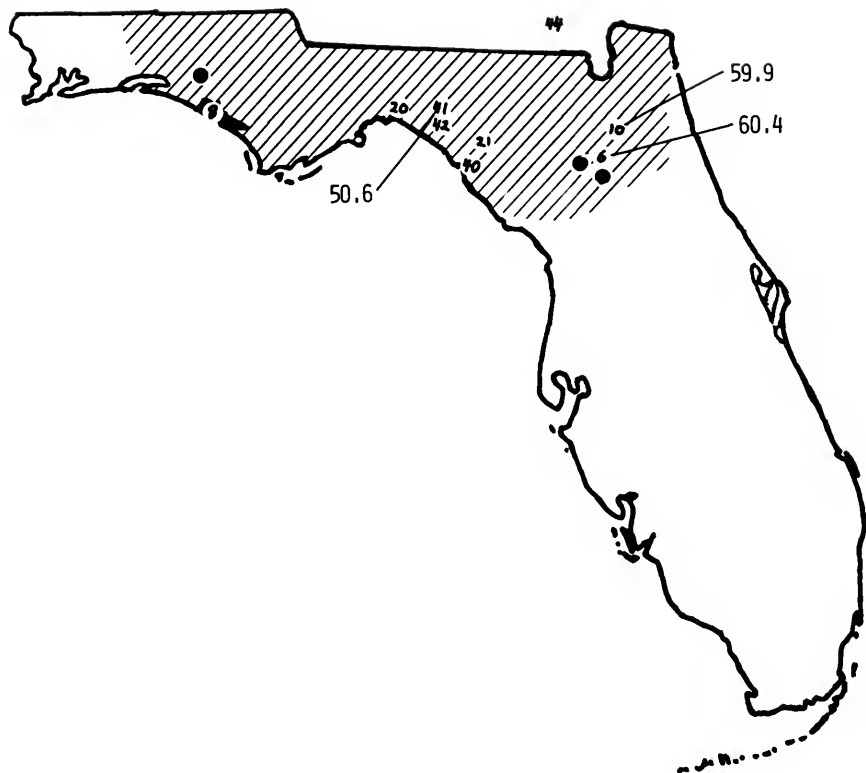


Fig. 6. Distribution of *Pictonemobius* sp. 525 in Florida. Hand printed locality numbers refer to numbered sites in Table 1. Additional localities are indicated by unnumbered dots. Mean pulse rates for localities with 3 or more individuals assayed (Table 1) are to the left and right of the Florida peninsula.

ECOLOGICAL DISTRIBUTION

General Habitat

Crickets of the genus Pictonemobius are found from dry sand dunes and central ridge areas to the margins of swamps and tidal salt marshes. They are rarely found in mature, dense hammocks with a closed canopy where fire has been excluded for 50 years or more. Most of Florida is maintained as a fire sub-climax with additional removal of pine from the central sand ridge area, clearing for agriculture, creation of pasture and range grazing land and road dredge and fill. In these disturbed areas I found the largest populations of Pictonemobius. Alexander and Thomas (1959) in their studies of three sibling species in the Allonemobius fasciatus group found that the three were mixed with no indication of interbreeding in areas where artificial clearing had taken place. Similar occurrences with Pictonemobius are discussed later in this chapter. The effect of burning on the size of Pictonemobius populations was evident in comparing the unburned and the annually and biannually burned plots of the Tall Timbers Research Station (TTRS) near Tallahassee, Leon Co., Florida. Here Pictonemobius were abundant along fire trails, roadways, and in plots that were burned as recently as within the last 6 months.

A plot which had fire excluded for the past 16 years did not contain Pictonemobius. They were scarce from the margins and absent from within the "woodyard hammock" which appears to have been undisturbed except for localized lightning fires and a record of logging in the northeast Gum Pond area in 1945. A 26 January 1913 account from the Beadel Diary records the "woodyard" as being "thick wood, tall pine, live oak, holly, magnolia, etc." (Betty Ashler, Historian, TTRS, Personal Communication, 10 March 1973).

Habitat descriptions of the four song types of Pictonemobius follow the classification of Laessle (1942).

The 531-D Habitat

Species 531-D is most common in xeric hammocks and in mesic and hydric hammocks that are burned or disturbed, thereby opening the canopy and thinning the understory. Many of Florida's ruderal communities such as old fields, fire lanes, roadside ditches, sand mounds, and lawns fall into this category making 531-D the most commonly encountered Pictonemobius. Species 531-D occurs in hammock communities over most of mid-central Florida even into "the sandhills" in the longleaf-pine and turkey-oak (Pinus palustris - Quercus laevis) association, predominantly beneath live-oak (Q. virginiana). They appear in xeric hammock to sandhill transitional zones where the forest thins out. Generally wire grass (Aristida stricta), bluejack-oak (Q. cinerea), laurel oak (Q. laurifolia), water-oak (Q. nigra), wild grape

(Vitis sp.), Virginia creeper (Parthenocissus quinquefolia), saw palmetto (Serenoa repens), and persimmon (Diospyros virginiana), are present in areas where large populations of 531-D are encountered. In Alachua and surrounding counties, they abound under several species of oaks, sweet gum (Liquidambar styraciflua), hawthorn (Crataegus sp.), persimmon, hackberry (Celtis mississippiensis) and wax myrtle (Cerothamnus ceriferus) growing solitarily or in small clusters in pastures and along grassy roadsides. They are also common in partially shaded lawns with some leaf litter and in and around clumps of fallen Spanish moss (Tillandsia usneoides) and on the well-drained portions of weedy-grassy roadsides and grown-over road dredge heaps. A typical 531-D hammock habitat, kept open by grazing cattle, is shown in Fig. 7.

The 531-B Habitat

Species 531-B is associated with the "scrub," i.e. the sand-pine and oak (Pinus clausa-Quercus spp.) association and longleaf-pine and turkey-oak association with some transition into longleaf-pine and bluejack-oak (Pinus palustris-Quercus cinerea) association. In most of these situations rosemary (Ceratiola ericoides), sand-pine (Pinus clausa) and gopher apple (Geobalanus oblongifolius) are very common and appear as the most consistent indicators of the presence of 531-B. The 531-B habitat is the central ridge sandhills on which the original longleaf-pine forest was present until



Fig. 7. Mesic hammock, southwest Gainesville, typical of 531-D habitat.

150 years ago. East and west coast isolates of 531-B occur on well-drained dunes, shell mounds, and dry sandy hills that contain live-oak (Quercus virginiana var. geminata) and sandhill plant associations. The more northern sandhills are more heavily forested and less likely to have sandpine, rosemary, and the cricket 531-B. The 531-B habitat is a xeric, open habitat, occupying the highest and best drained soils in the entire state. The "scrubby flatwoods" (Quercus var. geminata - Q. myrtifolia, Q. chapmanii) association which occurs " . . . in places where there is a slight rise of one or two feet above the general level of the flatwoods" (Laessle 1942) is usually not sufficiently open or well drained for 531-B.

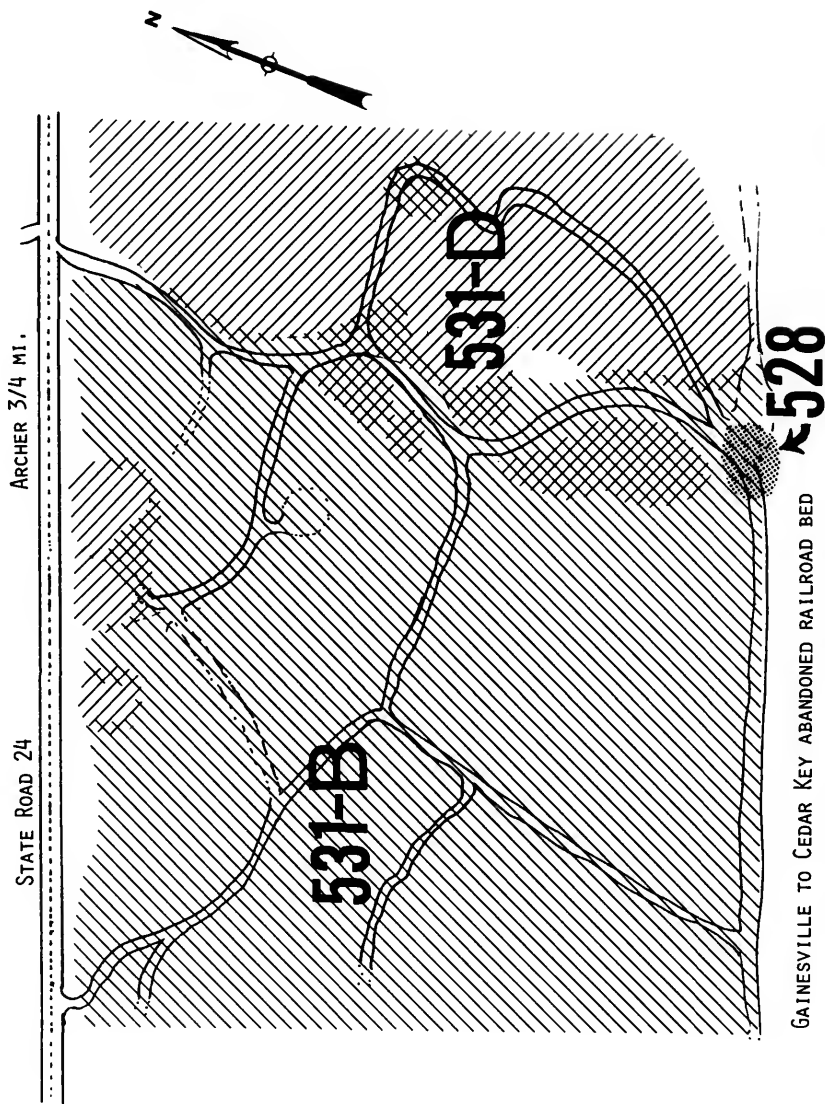
Species 531-D and 531-B were plentiful in an area where hammock woods adjoin a turkey-oak sandhill, 3/4 mi. west of Archer, Florida (Figs. 8 & 9). A similar distribution of 528 with 531-B occurred at a site .5 mi. west and .5 mi. north of Bronson, Levy Co., Florida (Figs. 10 & 11).

The 528 Habitat

Species 528 covers much the same geographic area as does 531-B but it occurs in the more disturbed, weedy, or recently burned sections of a site. Commonly 528 occurs spottily along a field margin, a road margin, the center strip of a dirt road, or in a dump. In a few cases isolated groups of singing males have been heard in the open near white sandy spots, surrounded completely by singing 531-B



Fig. 8. Aerial view of site $3/4$ mi. west of Archer, Alachua Co., Florida.
15 Feb. 1975. Turkey-oak (without leaves) left side, various oaks right side.



GAINESVILLE TO CEDAR KEY ABANDONED RAILROAD BED

Fig. 9. Distribution of *Pectenemobius* 528, 531-D and 531-B at site 3/4 mi. west of Archer, Alachua Co., Florida.



Fig. 10. Aerial view of site .5 mi. east & .5 mi. north of Bronson, Levy Co., Florida. 15 Feb. 1975. Weedy pasture top left, turkey-oak top right.

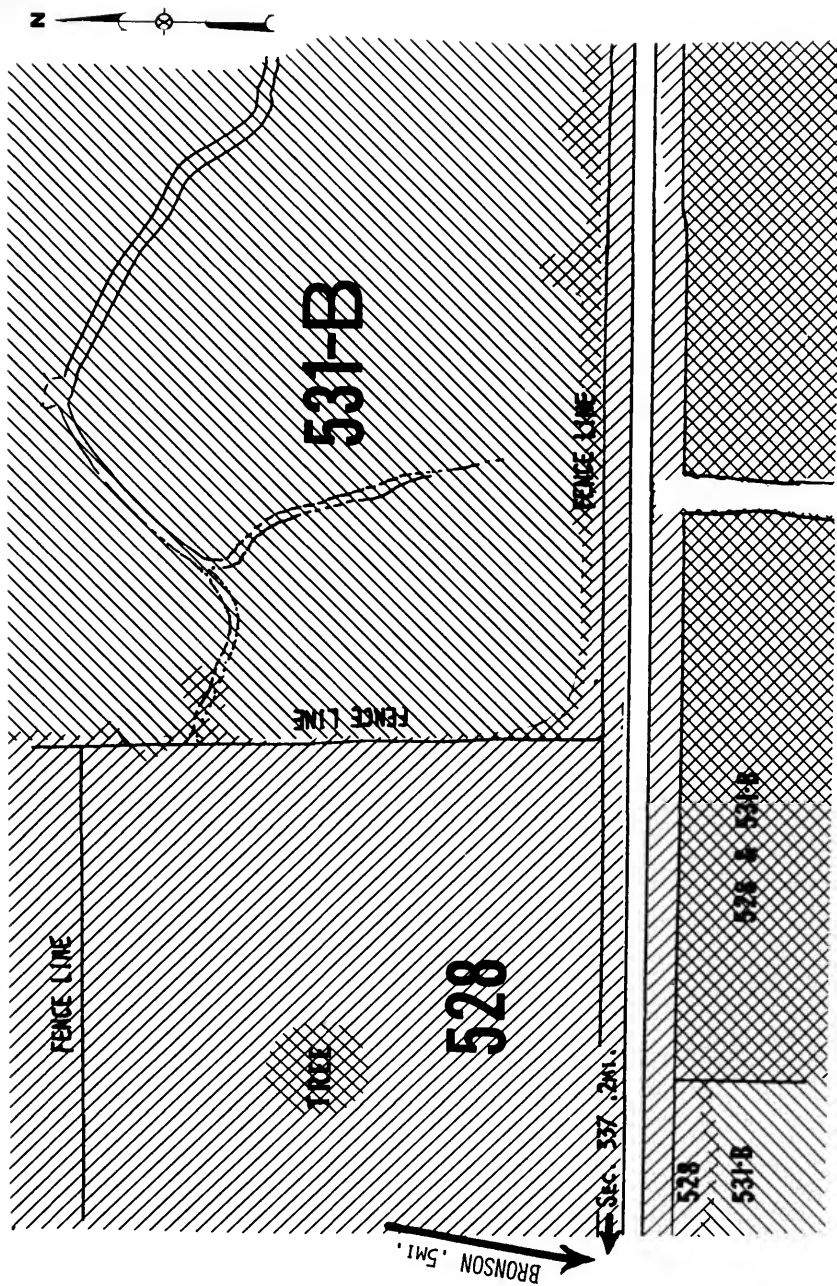


Fig. 11. Distribution of *Pictonemobius* 538, 531-B at site .5 mi. east and .5 mi. north of Bronson, Levy Co., Florida.

males (Fig. 9). The opposite situation, where 531-B is surrounded by 528 occurred in the center of a large weedy field (Fig. 11). Large numbers of 528 have been found in recently cultivated fields, weedy and grassy pastures, and in young pine plantations which were formerly part of, and now border, longleaf-pine and turkey-oak woods containing 531-B as shown in Figs. 10 & 11.

In the northern Florida counties 528 appears closely associated with disturbed pine forests that contain some turkey-oak. Here they often border 531-D areas with 528 predominating in the higher sandhills that are kept clear of underbrush by fire or mechanical means. A detailed study of a 528, 531-D habitat is presented later in this paper.

The 525 Habitat

Species 525 occurs in the slash-pine flatwoods (Pinus palustris) association, and in the black-pine and fetterbush flatwoods (Pinus serotina - Desmodium) association. These associations often border bayheads or extend outward in river flood plains and contain wax myrtle (Certhium ceriferus), wire grass (Aristida spiciformis), gall-berry (Ilex coriacea), blackberry (Rubus betulifolius) and sundew (Drosera capillaris). Species 525 sites have rich soils usually with a packed mat of dark colored pine needles, mossy patches, and openings in the wire grass with occasional depressions (left by uprooted trees) that often contain water during rainy periods. Fine grasses, sedges, and other

low herbage often grow in these depressions. Alachua Co. sites include northeast Gainesville's wet flatwoods that have been opened by occasional burning and clearing. Similar sites occur northward into the Okefenokee Swamp region of south Georgia. The river flood plains and low ground situations of the Florida panhandle are additional areas where 525 occurs. It is possible that species 525 occurs further northward throughout the pine flatwoods of Georgia, since this habitat is fragmented in North Florida into east and west coast areas separated by the central sand ridge.

The 528, 531-D Habitat, a Case Study

The temporal and spatial distribution of 528 and 531-D was intensively examined in an area near the Gainesville municipal airport (NE 1/4 of Sec. 24, R20E, T9S in August 1971). The study area was selected because it contained both 531-D and 528 over an ecologically diverse area. Components of xeric, mesic, and hydric hammock communities plus longleaf-pine and turkey-oak, longleaf-pine and bluejack-oak communities, both disturbed and undisturbed, occur together in this study area. The distribution of the principal types of vegetation are shown in Fig. 12. The woods area was a mixture of turkey-oak and longleaf-pine with bluejack-oak, water-oak, and wild cherry in one zone. Patches of palmetto were common throughout most of the woods and along the margin. Some low brush such as blackberry and

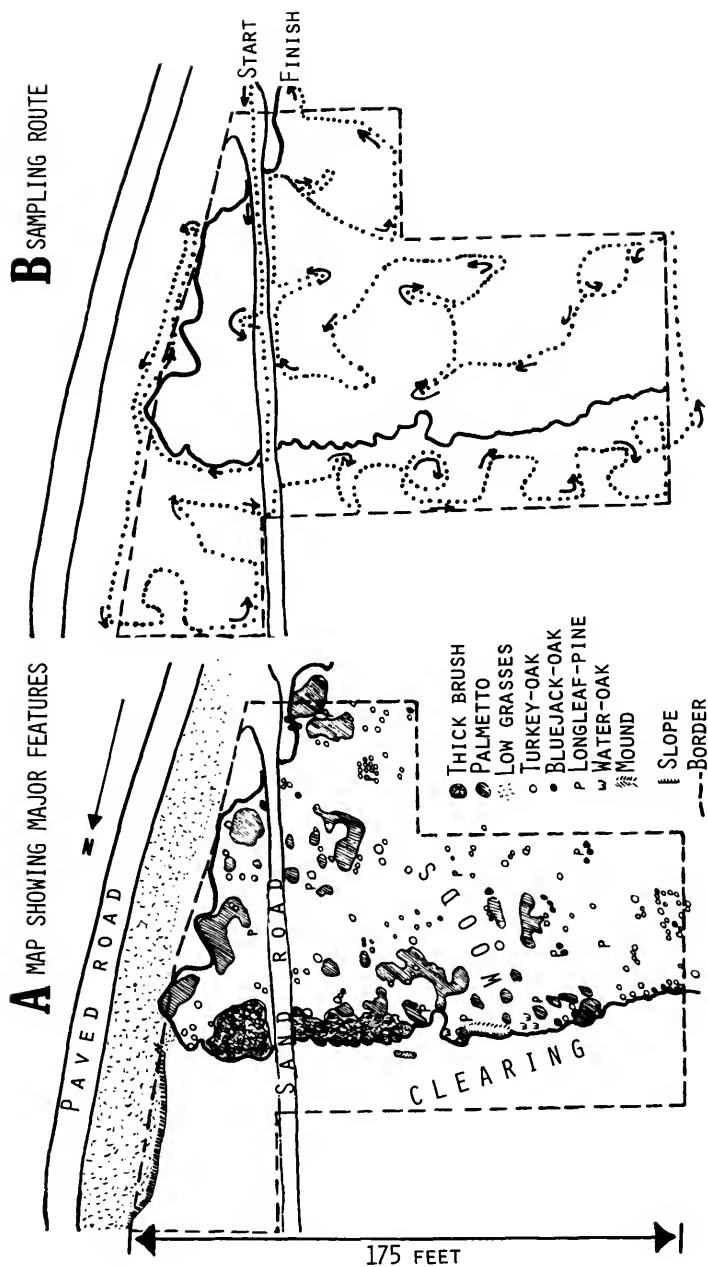


Fig. 12. Municipal airport site, Gainesville, Florida.

sumac is overgrown with grape (*Vitis*), Smilax, and virginia creeper (Parthenocissus quinquefolia).

The area where trees and brush had been cut close to ground level appeared to have been periodically treated in this manner for at least the last 10 years judging from a U.S. Government (1955-1960) aerial photo loaned to me by Dr. James E. Lloyd. The most recent clearing was about 6 months beforehand and resulted in about 30% bare ground. The remainder was littered with dead, cut turkey-oak and water-oak brush, palmetto fronds, and numerous heaps of bottles, paper, cans, and other debris.

Daytime high temperatures in the shade at 1 ft. above the ground were $33 \pm 2^{\circ}\text{C}$ on 20, 21 and 22 August, $31 \pm 2^{\circ}\text{C}$ on the 23rd and the 24th, and about 27°C on the 25th. Nighttime low temperatures were $20\text{--}22^{\circ}\text{C}$. The midday low relative humidity was 25-30% on the first 2 days, but increased to 50-60% on the remaining days.

Methods

An irregular plot approximately one acre was mapped with respect to the major physical features and vegetation (Fig. 12 A). Hourly surveys were made along a predetermined route (Figs. 12 B) over much of the period from 1:00 p.m. 20 August to 9:00 p.m. 25 August 1971. Sampling continued during periods without rain until 3 samples were compiled for each hour from 6:00 a.m. to 8:00 p.m. and one hourly observation was made for each hour from 9:00 p.m. to 5:00 a.m.

The 1624 locations of individual singers (528 and 531-D) were recorded on separate hourly maps.

Song Periodicity

Song production was diurnal and bimodal. The number of calling males increased during the early portion of the day but dropped to about 0.2X (528) and 0.5X (531-D) of the morning peak by midday. The number of calling males increased again in the afternoon (Fig. 13) but by dark the numbers of calling males of both 528 and 531-D had again decreased. This bimodal peak of the number of calling males agrees closely with a plot of the calling song produced by two isolated 528 males under conditions of constant temperature and controlled photoperiod in the laboratory (Fig. 14). Similar bimodality of singing occurs on sunny days (Figs. 15 A-C), on cloudy days (Figs. 15 D-F), and under uniform diurnal light intensity in the laboratory (Fig. 14) suggesting an internally controlled diurnal cycle of song production. Alexander (1960) states "Light intensity seems to be the most universally important single factor in determining the exact time on each day when different species begin song" (p. 42). This seems appropriate for nocturnal and crepuscular singing species, but does not offer a suggestion as to how Pictonemobius spp. "anticipate" the late afternoon peak of song production under uniform light (Fig. 14).

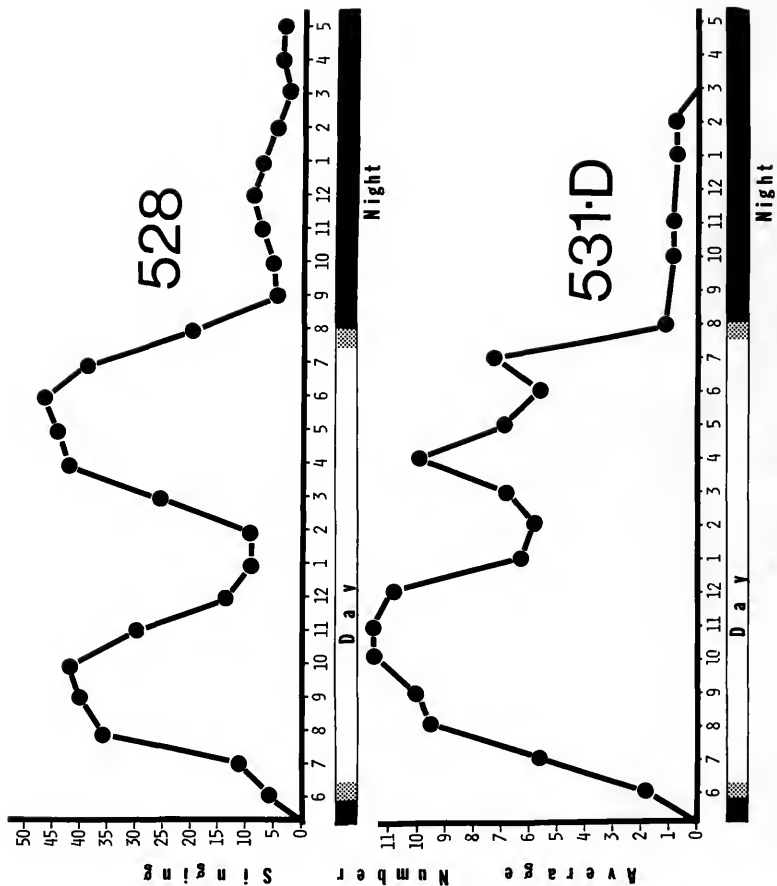
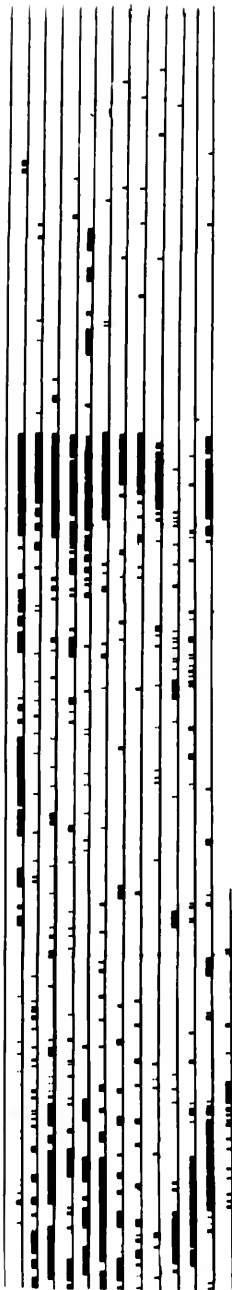


Fig. 13. Daily activity cycle of Pictonemobius 528 and 531-D, municipal airport site, Gainesville, Florida.

528 Male 1



528 Male 2

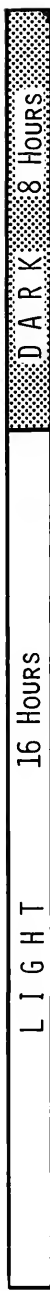
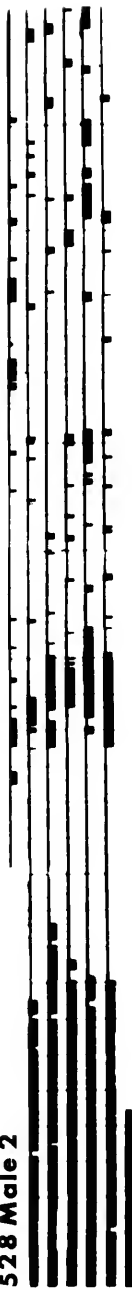


Fig. 14. Daily activity cycle of *Pictonemobius* 528 under laboratory conditions. Male 1 was reared to adult in the laboratory $25 \pm 3^\circ\text{C}$, 16L:8D photoperiod from a female collected 10 mi. north of Gainesville. Recording began at time of eclosion. Male 2 was field collected at the municipal airport site, Gainesville. Recording began 21 days after maintenance in the laboratory at $25 \pm 3^\circ\text{C}$, 16L:8D photoperiod. Recordings made at $25 \pm 1^\circ\text{C}$, 16L:8D photoperiod.

Spatial Distribution

Calling males of Pictonemobius 528 were heard in both open areas and wooded areas. Males of 528 in open areas decreased their calling at the approach of midday more than 10X compared with those in the wooded areas which decreased by only 2X (Figs. 15 A, B, D, & E). There was no indication of any movement to or from the woods at this time, though individual 528 males and females were observed moving just after rain, and on moist ground.

Calling males of Pictonemobius 531-D were usually in the woods, with only 5 out of 339 heard, located in open areas. The distribution of 528 singers on sunny days, (Figs. 15 A, B, & C) approximated the distribution of singers on cloudy days, (Figs. 15 D, E, & F) with the following exception: in the morning and afternoon on the cloudy days (Fig. 15 F) there appeared to be more singers in the open areas.

The likelihood of hearing courtship songs is independent of the number of calling songs at any given time. For 528, the highest proportion of courtship songs to calling songs occurs at night when the relative numbers of calling songs are low, and yet the relative numbers of courtship songs heard at night (7 in 9 sampling periods) approximates daytime counts (28 in 45 sampling periods). Courtship was recognized only once in 339 531-D songs as compared with 34 times in 1285 528 songs. Other 531-D courtship songs

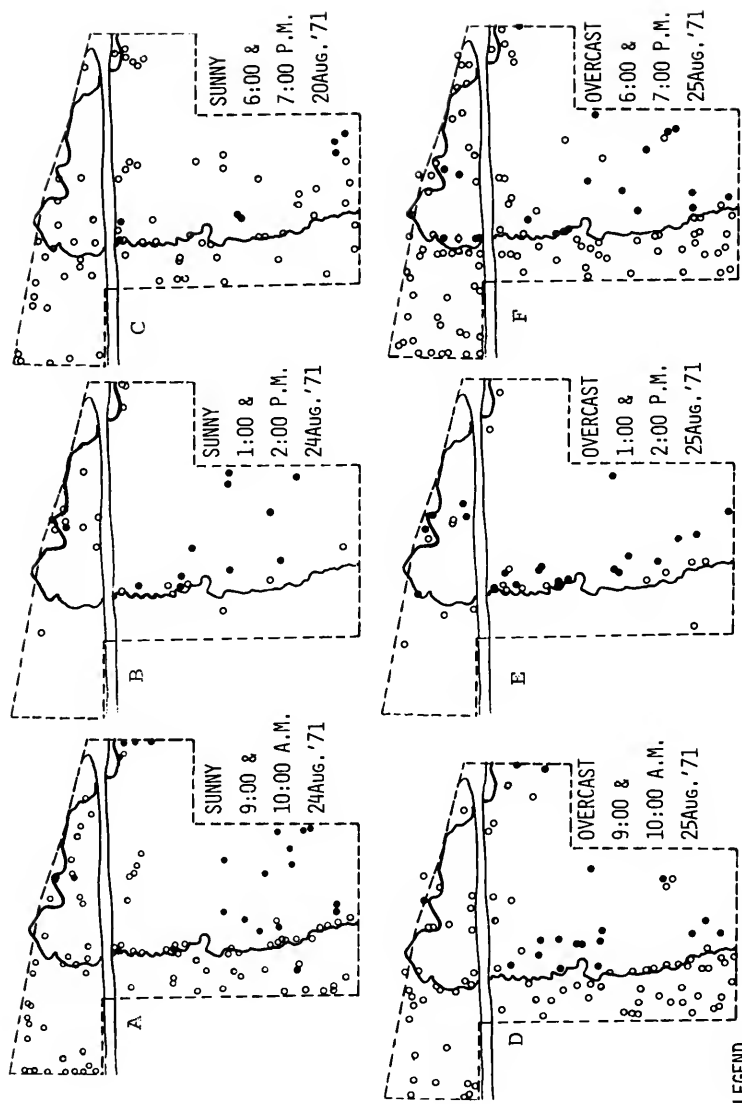


Fig. 15. Spatial distribution of singing *Pictonemobius* 528 and 531-D, municipal airport site, Gainesville, Florida.

may have gone unnoticed since the shorter [than calling] slow pulsed courtship song of 528 is more easily recognized in the field than the courtship song of 531-D.

Pulse Rate Overlap in Calling Songs

The four species of Pictonemobius are distinguishable from one another in the field on the basis of the male calling songs. When one first arrives at a new site it may be initially difficult to identify the singers but soon one detects the differences between the songs of the species involved, and in a short time can identify all of the singers heard. Once the listener is "tuned in" to the species-specific song differences, variation in pulse rate between open sunny sites and shady sites can often be detected. It is this difference in individual pulse rates, due to differences in microhabitat temperatures, that prompted my postulating the existence of overlapping pulse rates between species singing together. If such overlap should occur, heterospecific attraction could occur--for example, attraction of cool 531-D females to warm 528 singing males. To find out if such overlap in pulse rate occurs, I made measurements on clear winter days in hopes of finding a variety of ambient temperatures at ground level where crickets are located. Recordings of temperatures at various microhabitats during a cold clear winter day (Fig. 16) revealed a wide range of temperatures in places where crickets might be singing.

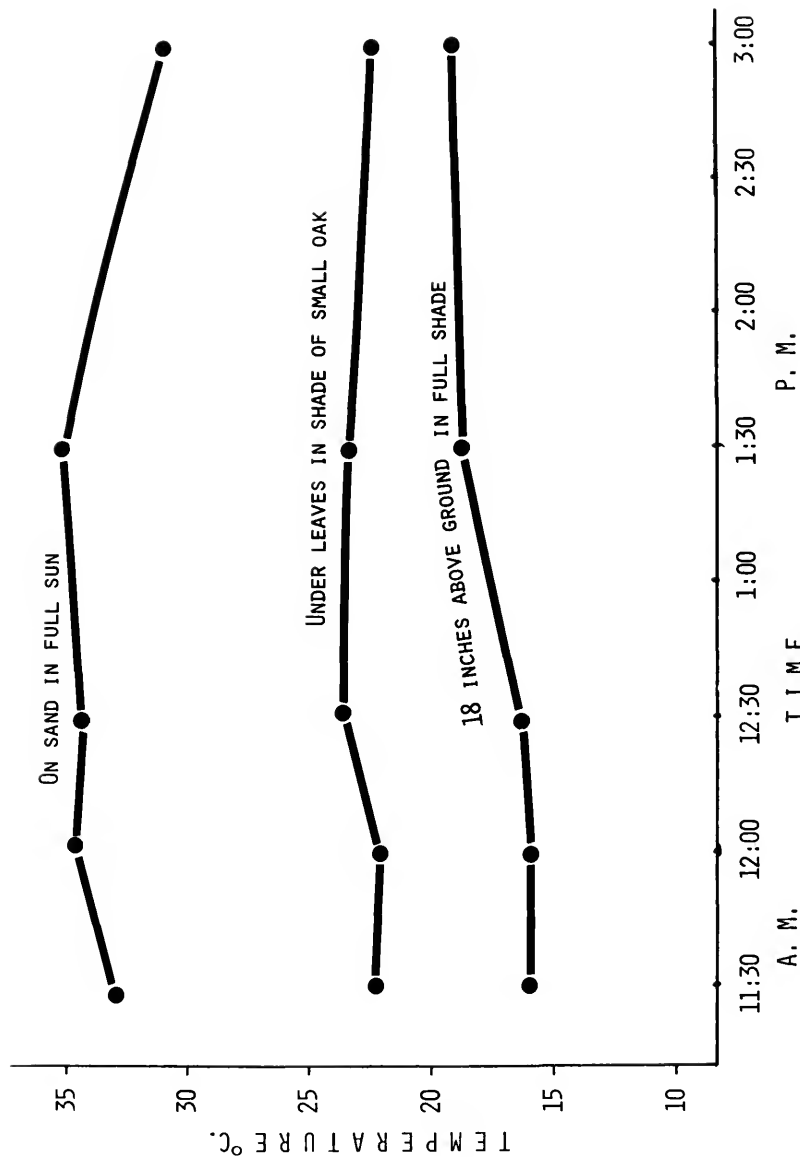


Fig. 16. Daytime temperatures of various microhabitats in close proximity, site 3/4 mi. west of Archer, Alachua Co., Florida. 5 March 1971.

Pulse rate overlap was investigated at three different sites where two Pictonemobius species were known to occur sympatrically. Calling songs of the fastest individuals of the slowest pulse rate species and the slowest individuals of the fastest pulse rate species were sought out and recorded to establish whether pulse rate overlap exists under these conditions in an area of approximately 100 square yards.

One study site was a portion of the transitional habitat used in the song periodicity study at the municipal airport, Gainesville. A cool, clear day with temperatures 15-20°C in the shade and 30-35°C under leaves in full sunlight was selected. Songs of 9 individuals of 528 and 6 of 531-D were recorded over a 1-hour period. Whenever possible the specimens were captured and the location of each singer noted. During the survey period the temperature on the ground in full shade went from 17.0 to 17.2°C while the temperature under a leaf in full sunlight remained at 32.0°C. The results are given in Table 2.

A similar 2-hour study was conducted on a site near Croom, Hernando Co., Florida, with 531-B (n=9) and 528 (n=10) that were found together in a disturbed, weedy, partially logged-over, longleaf-pine and turkey-oak area. The temperature at 18" above the ground in complete shade ranged from 14.6 to 15.0°C while the temperature in full sunlight at ground level ranged from 38.8°C to 40.4°C during

Table 2. Pulse rates of calling songs from field recordings of Pictonemobius 531-D
and 528, municipal airport site, Gainesville, Florida. 4 May 1971, 9:15
to 10:15 a.m.

Degree of shade in area where song was heard	Song Type 528			Song Type 531-D		
	n	X	SD	n	X	SD
None	2	44.8	.9	1	59.4	—
Partial	7	42.9	4.4	2	56.4	1.1
Shaded	0			3	53.6	6.6

the study period. The temperature under a leaf in full sunlight at 11:45 a.m. was 41.6°C but dropped to 25.2°C by 2:00 p.m. as shadows from nearby trees shaded it. The results are given in Table 3.

A similar 3-hour investigation was conducted with 531-D (n=16) and 531-B (n=21) at a site 3/4 mi. west of Archer, Florida, in an ecotone between longleaf-pine and turkey-oak sandhill and a live-oak hammock (Table 4).

At the Archer site one case of pulse rate overlap occurred between specimens identified by chirp length as 531-B and 531-D. This 531-D male was singing in the open and had a pulse rate of 66.6 p/s which was 1.4 to 7.2 p/s faster than the four slowest 531-Bs for that hour. There is no correlation between pulse rate and degree of shading where the song was heard: however, most specimens of 531-D were in more shaded situations than those of 531-B.

By assuming a linear relationship between pulse rate and temperature (Walker 1962) and by using the mean pulse rate of conspecific laboratory recorded individuals from the same locality as a reference, the temperature of each singing male was approximated. The results indicate that calling males are in areas where temperatures are 25-35°C even though a wider range of temperatures are available as broadcasting sites. Considering that individuals vary in calling song pulse rate at any given temperature, the range of temperature values derived from the field recordings

Table 3. Pulse rates of calling songs from field recordings of Pictonemobius 531-B and 528, near Croom, Hernando Co., Florida. 8 March 1971.

Degree of shade in area where song was heard	Song Type 531-B			Song Type 528		
	n	X	SD	n	X	SD
			Range			Range
<u>Hour 1 (11:45-12:45)</u>						
None	5	63.2	1.6	2	46.2	.5
Partial	0			3	45.5	2.1
Shade	1	50.8	—	0		
<u>Hour 2 (12:45-1:45)</u>						
None	1	66.0	—	2	46.2	2.5
Partial	3	59.1		3	46.5	.6
Shade	0			0		

Table 4. Pulse rates of calling songs from field recordings of *Pictonemobius* 531-B and 531-D, 3/4 mi. west of Archer, Alachua Co., Florida. 5 March 1971.

Degree of shade in area where song was heard	Song Type 531-B				Song Type 531-D			
	n	X	SD	Range	n	X	SD	Range
<u>Hour 1 (11:45-12:45)</u>								
None	7	68.6	6.6	59.4*-75.0	2	61.8	6.7	57.1-66.6*
Partial	2	72.3	2.4	70.6-74.0	0			
Shaded	3	67.7	2.3	65.2-69.7	0			
<u>Hour 2 (12:45-1:45)</u>								
None	1	67.4	—	—	1	54.5	—	—
Partial	0		—	—	6	61.3	4.2	56.1-64.5
Shaded	1	70.6	—	—	4	45.0	2.9	42.3-48.0
<u>Hour 3 (1:45-2:45)</u>								
None	3	67.2	2.4	64.5-69.0	0			
Partial	4	66.6	2.9	64.5-70.6	1	45.8	—	—
Shaded	0	—	—	—	2	45.7	.1	45.6-48.8

*Individuals not collected had to be identified by the number of pulses in the chirp, and such identifications are usually, but not always, correct. It is possible that a 531-2 cricket responsible for the apparent overlap in pulse rate was wrongly identified.

Table 5. Estimated temperatures ($^{\circ}\text{C}$) of field recorded male Pictonemobius determined by assuming a 2.2 p/s increase in pulse rate for each degree rise in temperature.

Song type	Municipal airport site 4 May 1971, 17-32 $^{\circ}\text{C}$ *				3/4 mi. west of Archer 5 March 1971, 15-42 $^{\circ}\text{C}$ *				Nr. Croom, Hernando Co. 8 March 1971, 15-35 $^{\circ}\text{C}$ *			
	n	\bar{X}	SD	Range	n	\bar{X}	SD	Range	n	\bar{X}	SD	Range
528	9	27.1	.89	25.6-28.4					10	30.3	3.81	28.8-31.0
531-D	6	30.1	1.50	28.5-32.1	16	28.3	.13	23.7-32.4				
531-B					21	32.5	2.10	28.4-36.7	9	31.5	2.2	26.9-33.7

*Temperatures measured at ground level in places where crickets might sing.

(Table 5) may actually be less than given. Furthermore, the species with the fastest pulse rate appeared to be singing at the highest temperature at each of the three localities studied. This would tend to accentuate the calling song differences that already exist between the song types at each of the three study sites. The primary conclusion from this study is that calling song pulse rate overlap in areas of sympatry is extremely rare.

Coldhardiness Study

All life stages of Pictonemobius have been found during all seasons of the year, and yet during winter months or at drier times early juveniles appear scarce. Possible reasons why early juveniles become scarce include the lack of female oviposition, delayed egg development (egg overwintering), behavioral adaptation (i.e. burrowing), or the eggs or juveniles being unable to survive periods of severe cold or drought.

Laboratory vs. Field 531-D Coldhardiness Test

Pictonemobius spp. breed continuously, all stages being present throughout the year, even in areas of northern Florida where weather service winter temperatures below -8°C occur yearly. Pictonemobius 531-D survives winters in the Gainesville area, where ambient air temperatures below -8°C are frequently recorded. To determine whether field-collected Pictonemobius 531-D were physiologically better adapted to survive cold than laboratory-reared

colonies of the same species, and which life stages were the best adapted if any, the following study was conducted. From both laboratory-reared colonies and recent field collections (April), ten individuals of five classes--small juveniles, (large) juvenile males, (large) juvenile females, adult males, and adult females--were placed in rearing jars and put in an environmental chamber to be subjected to a series of successively colder night temperatures, approximately 10 hours each night, until all the crickets had died. Each midday, at approximately 20°C, mortality counts were made.

In general laboratory-reared 531-D suffered more mortality beginning at -4°C than the field-collected individuals (Table 6). It appears that small juveniles were the least tolerant of low temperatures. This experiment was in part repeated with 10 male and 10 female nymphs from the same field and laboratory sources 2 days later. A single 10-hour cold period of -8°C was given the first night to eliminate effects of starvation and dessication which were suspected to have developed in the previous experiment. All test crickets were dead the day following treatment suggesting that a single 5-hour exposure to -8°C was sufficient to kill 531-D collected in the field. Under natural conditions 531-D would rarely have to contend with temperatures below freezing.

Interspecific Coldhardiness Test

The difference in cold hardiness among field-collected

Table 6. Coldhardiness of field-collected vs. laboratory-reared Pictonemobius 531-D. Coldhardiness expressed as number alive on day following treatment.

Life stage	Number surviving nighttime low temperature††						
	Field collected			Lab reared			
	-1	-4	-7	-9	-1	-4	-7
Small juvenile	10	10	0	0	8	5**	0
Juvenile male	10	10	3	0	10	6	1
Juvenile female	10	8	0	0	10	7	3
Adult male	10	10	5	1†	10	8	5**
Adult female	7*	7	1	0	10	10**	1**

*n=7 at start

**barely moving at time of census at $\approx 20^{\circ}\text{C}$

†died next day

††temperature: ambient air inside test chamber, held at low for a 5 hr. minimum

528, 531-D, 531-B, and 525 were investigated. In early May 1971, varying numbers of field-collected individuals of each species were divided into adult male, adult female, and juvenile groups, placed into rearing jars containing sand that was moistened on one side of the jar, and a small piece of paper toweling. All jars were placed in the environmental chamber, which was set to provide midday high temperatures of 17°C followed by successively lower nighttime temperatures. On successive nights the temperature declined and was held for four hours at +3, -3, and -8°C. Censusing took place during the following midday warm-up periods.

The stepwise decline was to give the greatest chance for acclimation to occur as well as to provide more than one period where the temperature might be low enough to cause mortality. The temperature at the towel-sand interface, where most of the crickets congregated, was monitored during most of the cooling-down and warming-up periods and showed a 1- to 2-hour lag in reaching the same temperature as the ambient air in the environmental chamber.

A pretest census and the census following the first cold night (+3°C) were identical; no crickets died. The results of the successively colder nights on adult males, adult females, and juveniles of the four species of Pictomobius are in Figure 17. Species 531-D and 531-B appeared the least cold hardy with 525 and 528 holding near pretest

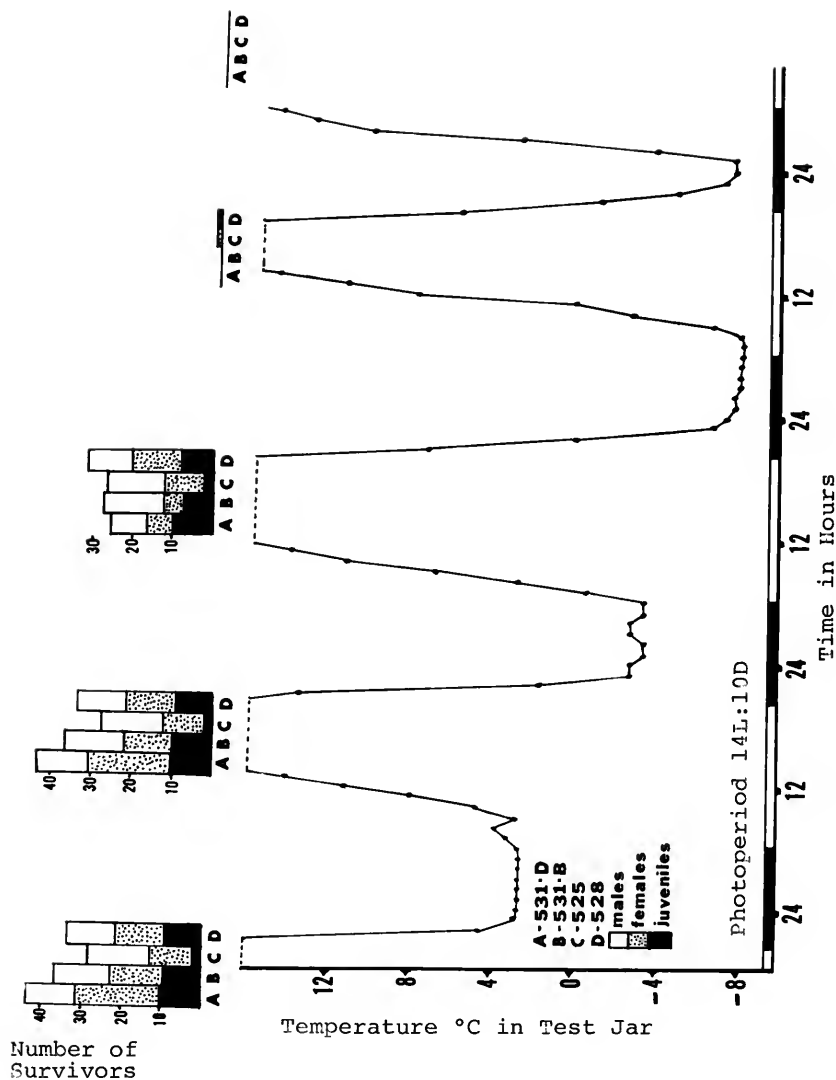


Fig. 17. Proportion of crickets alive following each of 4 successive cold treatments.

levels after exposure to -3°C . Only one juvenile 528 and one adult female 525 remained after an exposure to -8°C . One additional treatment of -8°C killed the remaining crickets. During these studies laboratory rearing of Pictonemobius continued normally. Crickets for controls in these experiments were not always available, but surplus crickets that were collected or reared, lived for weeks under laboratory conditions.

PHONOTAXIS TO CALLING SONGS

Introduction

Species specific "calling songs" or "pair formation songs" are produced by male Pictonemobius (and most other crickets as well) to attract sexually responsive conspecific females for mating. Phonotaxis is the directed movement of a female toward a sound. The strength of the phonotaxis that a female shows toward the source of a male calling song or test signal is difficult to measure. The development of a consistent and reliable method of quantifying female phonotaxis had to precede attempts to evaluate the specificity of phonotactic response. The development of such a method is a major part of this section.

The assay of virgin female Pictonemobius 528, 531-D, 531-B, and 525 for their response to a wide range of natural and synthetic sounds further defined these Pictonemobius as species.

Methods

Remote Event Recording Equipment

Recordings of song cycles and movement of crickets were made on an Esterline Angus model A620T multichannel event recorder (ER). On-off gating was accomplished by an

Alton Electronics Company Sensitive Relay (SR). The following transducers were used to trigger the relay.

- (1) Microphone transducers: A number of inexpensive crystal microphones, such as the Thoro Test TRM-1A "tape recorder microphone," or dynamic microphones such as Astatic Corp. model DN-HZ studiomike were used. An increase in sound level such as a cricket singing caused the relay to trigger.
- (2) Cadmium disulphide photoelectric cell: This photocell was used to record the exact time that the LNR lights were switched on or off.
- (3) Phonocartridge: A "sensitive platform" was constructed from nylon mesh strung tightly across one end of a 6 x 2 inch hoop and held tight by a small spring pulling downward against a central 1/2 inch diameter metal disc, (Fig. 18). The needle of an Astatic type 414-2 phonocartridge rested lightly on this central disc. Vibrations applied anywhere on the platform were transmitted to the phonocartridge and resulted in triggering the relay-event recorder system. The relay could be activated by the slight stroking of a human hair. Whenever crickets walked onto or moved slightly while upon the platform, the relay was activated several times.

To preserve the relay contacts and to eliminate unnecessary pen movements of the event recorder, capacitors ranging from .94 to 50.0 μ f were applied to the relay to reduce the on-off switching rate. The capacitance was adjusted to cause the event recorder contacts to remain

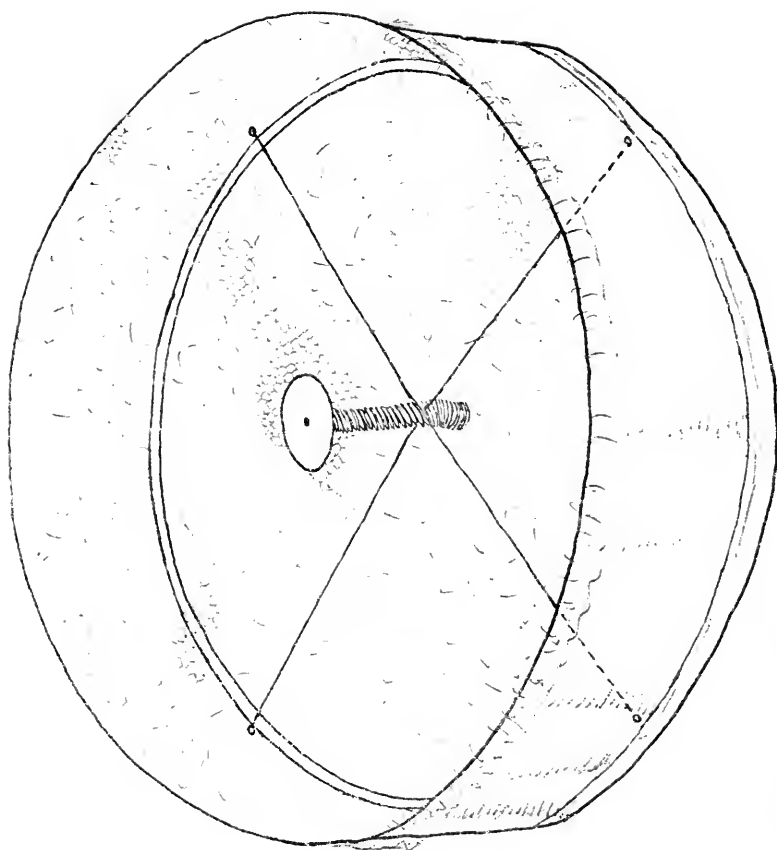


Fig. 18. Sensitive platform.

closed longer than the pulse interval, thereby remaining closed for the entire duration of a chirp. Further capacitance was often applied to cause the relay contacts to remain closed during chirp intervals, causing the recorder pen to remain in the "on" position until singing had stopped. Depending on the transducer and signal, various resistors with values in the 100 to 100,000 Ω range were applied across the relay input to locate relay sensitivity controls somewhere near their mid range. Both the capacitors and the resistors had the effect of preventing spurious noise from being an event on the ER chart and averaging discontinuous signals into continuous positive responses. The CDS Photocell required a 100 Ω resistor at the input and 50 μf at the output whereas most of the microphones were used with 76,000 Ω , 10 μf or 100,000 Ω and 5 μf , across the input and output respectively.

Synthesis of Artificial Test Signals

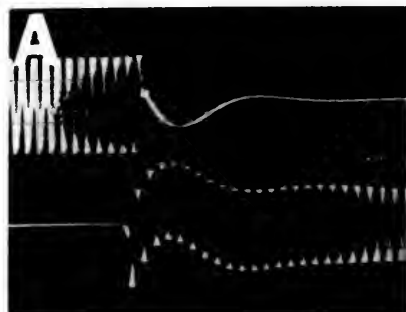
Cricket songs generally have their energy concentrated at a single frequency between 3,000 and 8,000 Hz and consequently the sounds they produce are often musical or "bell like" to the human listener. This single frequency is the result of rapid wing vibration developed as the wing file teeth are driven over the scraper during a wing closure. The natural calling songs of Pictonemobius are described in the previous section.

In synthesizing cricket signals a Hewlett Packard 201C Audio Oscillator (AO) was used to generate a pure tone of

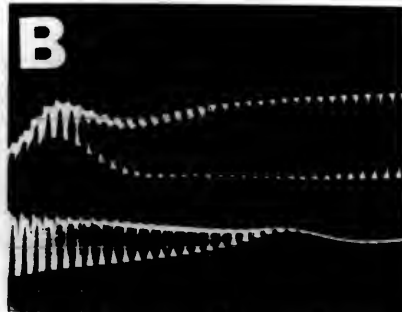
7,000 Hz. This tone was switched on and off by a General Radio type 1396-A Tone-burst Generator (TG) to create a trill with an on-off ratio of 1:2. The AO output was monitored by a Monsanto model 100B Counter Timer which gave a visual readout of the AO frequency at rapid intervals. A sine wave generator (SWG) was used as a timing input for the TG and used to vary the pulse rate. The signal thus produced had on-off switching noise with a harsh on-off contrast. This type of signal was used once to test females for response to synthetic signals (Fig. 19).

Further refinements involved replacing the TG with an Alton Electronics Company¹ Field Effect Transistor Gate Signal Switch (FET) which switched the 7,000 Hz AO signal on and off. An externally applied drive signal produced by an Alton Electronics Company timer determined the FET switching rate. The rise-time and fall-off of each pulse was modified by application of a .04 μ f capacitor across a second drive input of the FET. This equipment made it possible to shape the beginning and end of each pulse (Fig. 19 B). An example of an artificial signal is illustrated in Fig. 19 D along with a natural pulse (Fig. 19 C). The TG was used to chop this signal into chirps various numbers of pulses long. The output from the

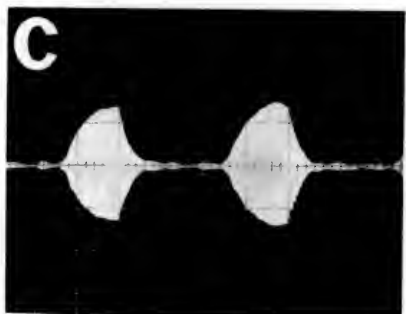
¹The Alton Electronics Company is presently out of business. Alton Higgins of Archer, Florida, developed and marketed the equipment sold by Alton Electronics Company.



END AND BEGINNING OF
"SQUARE CUT" PULSE,
SYNTHETIC SIGNAL, 7000 CPS.
.5 MSEC/DIV



BEGINNING AND END OF
"ROUND CUT" PULSE,
SYNTHETIC SIGNAL, 7000 CPS.
.5 MSEC/DIV



PAIR OF NATURAL PULSES, 5 MSEC/DIV



PAIR OF SYNTHETIC PULSES, 5 MSEC/DIV
7000 CPS.

Fig. 19. Characteristics of square cut, round cut, natural and synthetic pulses.

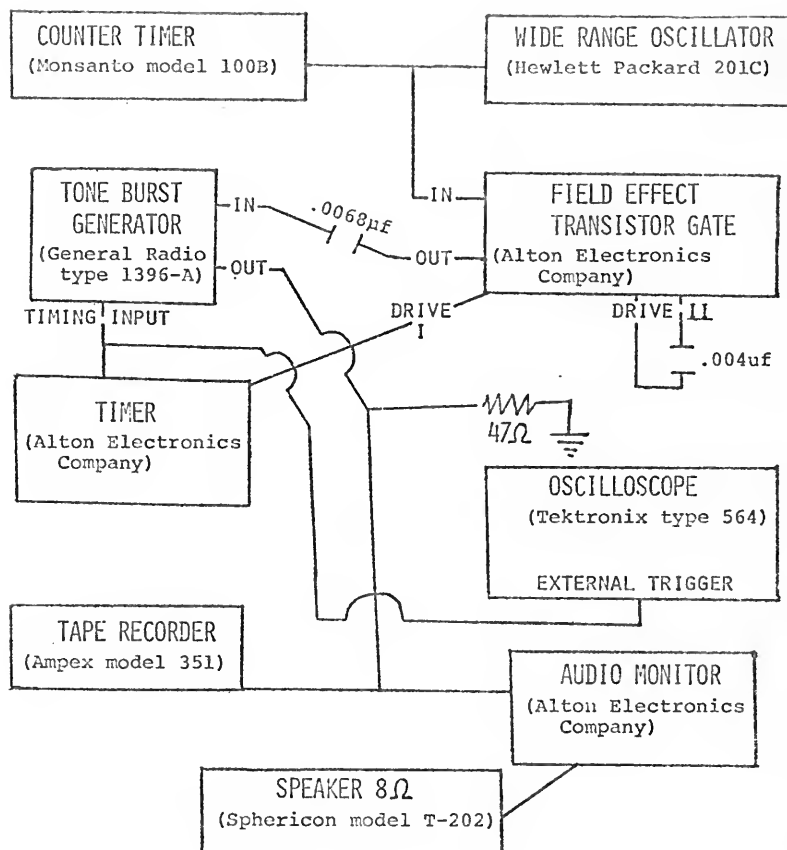


Fig. 20. Schematic of equipment used in production of synthetic cricket calls.

TG was displayed on the Tektronix where final adjustments were made upon the amplitude of the AO output, pulse rate, pulse interval, and pulse shape. The finished signal was switched to the input of the Ampex and recorded on tape at 15 ips. A section of this tape was then removed and made into a loop for testing females for phonotaxis. Sphericon model T-202 (Sphericon) or Realistic 40-2338 (Realistic) exponential horn tweeters (8 Ω) were used to broadcast all signals (Fig. 20).

Equipment for Tests of Phonotaxis

A 2-foot-diameter, sand-bottom arena with a 6-inch-high screen side and a lightweight nylon-mesh lid was the test enclosure in which female-responses were studied (Fig. 21). Sitting atop a 6-foot step ladder, the experimenter looked downward on the arena, recorded data, and by remote controls started or stopped the broadcast of sound to an arena speaker. In the arena center were two or three water vials with exposed moist wicks and a small dish of crushed dogfood.

All arena experiments took place in the low noise room (LNR) under a 16L:8D photoperiod. All experiments were at $25 \pm 1^\circ\text{C}$ and 35 to 50% RH.

The Ampex was used to record and play back all tapes for analysis and bioassay. Tape loops up to 20 feet in circumference were played on the Ampex by running the tape over additional idler pulleys. For each tape loop the

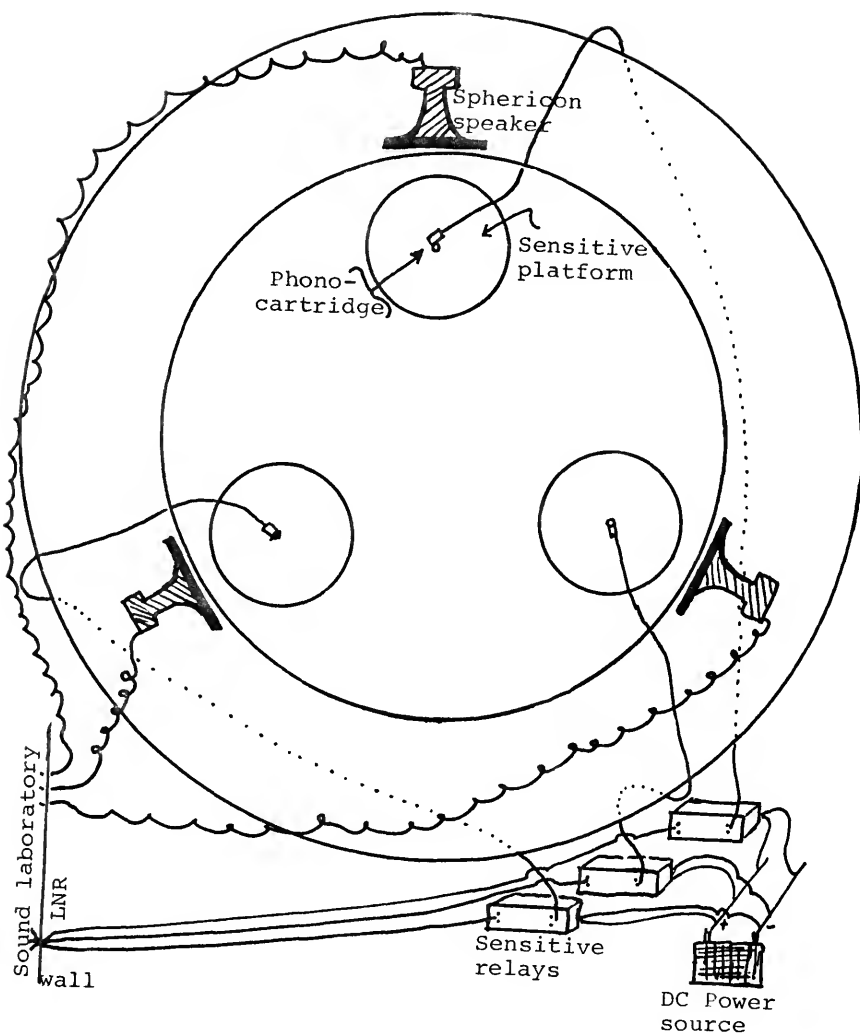


Fig. 21. Test arena containing 3 sensitive platforms connected to sensitive relays, with a speaker at each platform. The test signal₂ sound level was adjusted to 75 db (re. 0.002 dynes/cm²) at 6 inches in sound laboratory.

output of the Ampex was tested, and the sound level adjusted in the sound laboratory.

Experimental Designs

Controlled experiments demonstrating female response to natural or synthetic male calling songs have been reported for Oecanthus by Walker (1957), for Ephippiger spp. by Busnel (1963), Teleogryllus by Hill et al. (1972), and Scapteriscus by Ulagaraj (1974). It appeared that Pictonemobius would lend itself quite well to the bioassay of virgin female response since they are plentiful, small, wingless, and diurnal. The several pilot investigations into various factors and equipment that were necessary for a reliable, controlled test will not be described in detail, but some of these findings will be given to preface larger and more inclusive tests discussed later.

Early experiments of female response to sound level, response periodism, and to "square cut" synthetic trills were made with a single test speaker, located randomly in one of 16 speaker locations surrounding the arena (Fig. 21) with a "dummy" speaker placed opposite as a control. Two wire arcs were placed on the mesh lid of the arena so that when viewed from above an arc with a 6.5 inch radius extended outward from each speaker, demarking an area defined here as the "zone of attraction." Each zone included 10% of the area of the arena. Each test consisted of a 9-minute silent period followed by a broadcast

period of 9 minutes. Following this the speaker positions were changed and a different test sound was presented to the same crickets after another 9-minute silent period. Ten females were tested each time. If two or more females were within either zone of attraction another test speaker position was randomly chosen before the test was begun. The sound period was divided into three, 3-minute periods. The number of females in each zone of attraction (test and control) at the end of each 3-minute period was recorded. Control, or dummy, speaker counts were made in case females tended to respond visually to a speaker or remain beneath the wire arc.

Later experiments of female response to "round cut" trills and chirps was evaluated by using three test speakers, and the addition of ER counts of cricket activity. The random selection of speaker locations used in earlier experiments sometimes resulted in a test starting when several crickets were concentrated in an adjoining speaker location. To eliminate this, a sequential presentation of test and control signals was developed in which three speakers were spaced equidistant on the outer margin of the arena (Fig. 21). A control (natural calling song instead of the previously used silent control) and test broadcasts were presented alternately in a counter clockwise direction.

A 6-minute silent period preceding each 6-minute test signal enabled the experimenter to leave the low noise room,

change to the next tape loop and speaker position, and adjust the signal intensity. It also allowed enough silent time before the next test presentation for the experimenter to return to the room and for the crickets to resume normal movements around the arena after the experiment was readied. After each test signal presentation, a 3-minute silent period preceded each control tape loop presentation. Each 6-minute control broadcast had the effect of clearing the area around the next test speaker and the previous test speaker by attracting the test subjects to one location, and served as a before and after control signal, to which each test presentation could be compared. The 6-minute test and control periods allowed enough time to record response and yet present a number of different signals on the same day without loss of sensitivity and responsiveness on the part of the crickets. The sequence was as follows: 6-minute control signal, 6-minute silence, 6-minute test signal, and 3-minute silence. This sequence was repeated for each different test signal, and ended with a 6-minute control broadcast. In this manner it was possible to present a series of seven different test signals, in a randomly chosen order, to a group of virgin female crickets in less than 3 hours. By the end of the third consecutive day of testing, each test signal had been broadcast once on each of the three speakers, thereby eliminating speaker bias.

For the early tests of phonotaxis, the age of virgin females was the only standard used to select test subjects. Because some females showed a lack of responsiveness, a new method of selection of virgin females was developed. All females used in later experiments were selected only if they began a mating sequence (courtship to the "spermatophore formation" stage) (Mays 1971) with a male of their own song type 24-48 hours prior to testing. They were selected by taking a stridulating male, placing him in a jar with several virgin females, observing courtship, and then removing any responding female as soon as the male formed a spermatophore.

Differential Response to Taped Calling Songs

Species 528 and 531-D virgin females were tested for response to tape recordings of their own (conspecific) and each other's (heterospecific) calling songs for three reasons. First, such a test would determine whether virgin females would respond to tape-recorded songs of their conspecific males. Second, it would demonstrate if this response was species specific or whether they could be attracted to each other's songs. Third, it would give some indication as to the suitability of the test in terms of signal presentation, sound pressure level, and response behavior of the females tested.

Seven to ten virgin females of both 528 and 531-D were tested in the arena, one species at a time. A total of

25 to 28 females was tested in three replicates of each species. The numbers that responded by entering the zone of attraction of the test speaker are shown in Fig. 22. There was no indication of attraction to the dummy speaker. Such sharp discrimination by females in favor of the calling songs of their conspecific males demonstrates one way that 528 and 531-D avoid interbreeding. The two test signals were 528-100, 35-1 p/s at 26.0°C and 531-78, 44-8 p/s at 25-8°C.

Sound Level

A test to evaluate the response of virgin females to a more-intense-than-normal male calling song was necessary before an appropriate sound level for future LNR arena tests could be selected. The effect of a more intense signal on the phonotactic behavior of virgin females was evaluated and compared with a tape recorded 75 db song similar to that produced by singing males at 6.5-inch distance. A General Radio Company type 1551 B sound level meter (SLM) (scale A at 6.5 inches from the speaker), was used to adjust a tape loop copy of 528 calling song to two levels of intensity, 90 and 75 db.

The speed of female response to sound was greater during the 90 db signal broadcast than during the 75 db signal. The females would often jump with the first chirp of the 90 db test signal and run to the speaker, or move rapidly about, traveling in and out of the zone of

attraction. The 90 db test signal was effective in demonstrating a rapid and positive response, but the responding females moved around much more rapidly than ever observed in response to living males (Fig. 23).

The distribution of sound level in the arena was measured with the SLM. The zone of attraction closely approximated the area to which 75 db extends (Fig. 24). Broadcast sound levels of 75 db were chosen for all subsequent experiments because adequate response occurred in a relatively short period of time at sound levels approximating natural ones.

Response Periodism

Daily changes in female response were suspected in view of the daily rhythm of male song production. The response of ten, 3-week-old, virgin, laboratory-reared 528 females, to a pair of 9-minute broadcasts of taped calling song separated by 9 minutes of silence was measured four times daily for three consecutive days. Once daily the broadcasting schedule was offset by two hours resulting in broadcasts every 2-hour period of a (composite) 24-hour day.

In this study the percent of those entering the zone of attraction during the initial 3 minutes of broadcast were weighted 3x, the second 3 minutes of broadcast were weighted 2x and the final 3 minutes of broadcast 1x. The

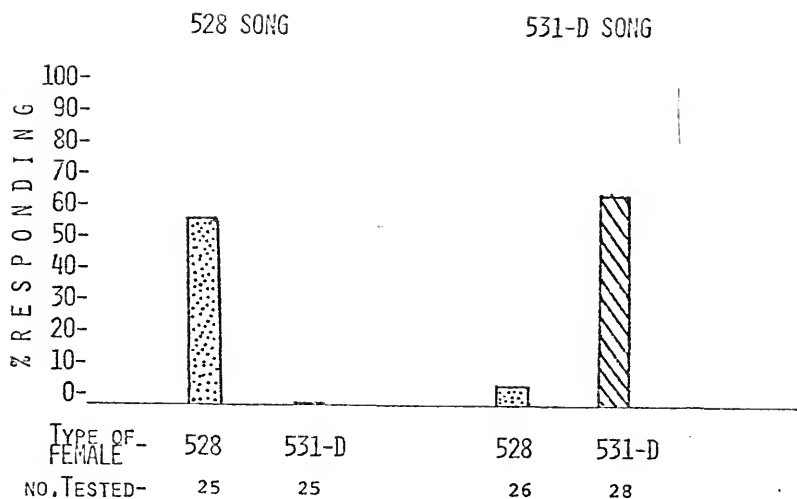


Fig. 22. Response to tape recorded calling songs by Pictonemobius 528 and 531-D females.

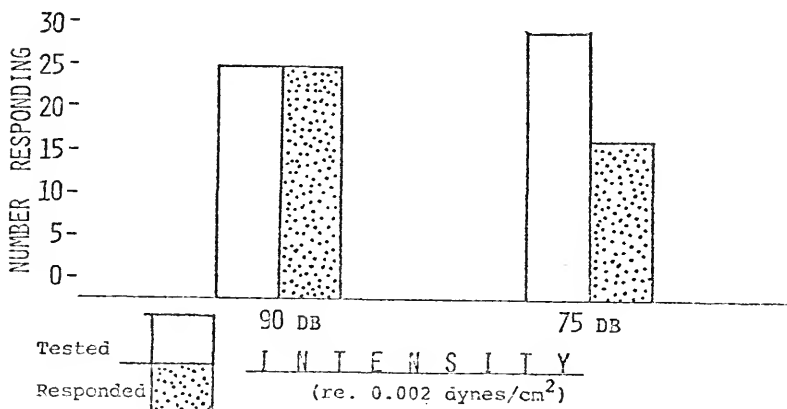


Fig. 23. Response of Pictonemobius 528 virgin females to 75 db and 90 db calling song sound levels.

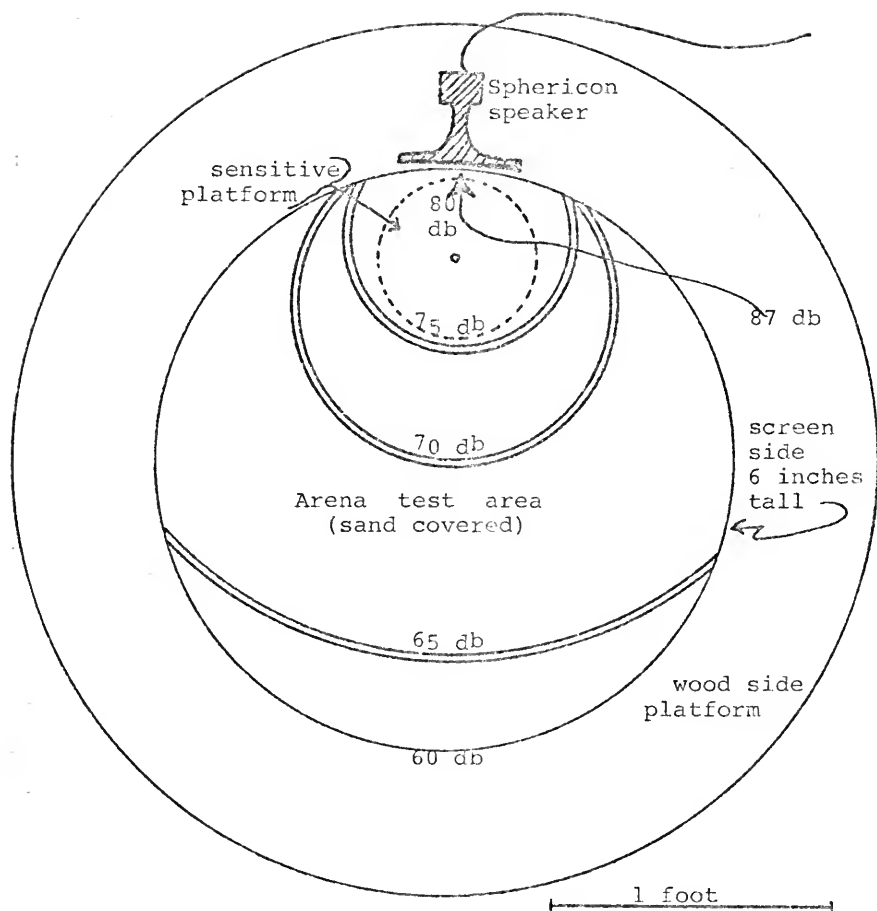


Fig. 24. Distribution of sound level in test arena.

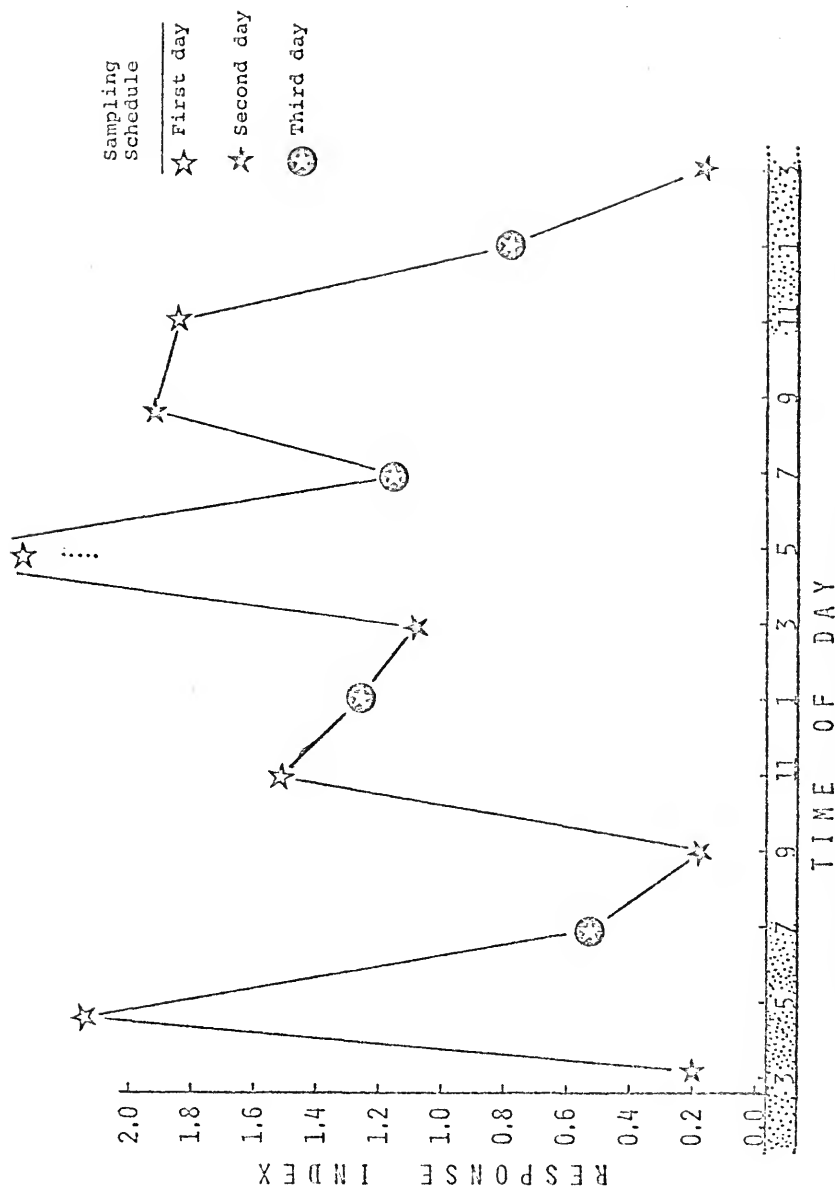


Fig. 25. Female response in relation to the time of day using *Pictonemobius* 528 natural calling song (528-100).

average response to the broadcast for the dark period (1.25) was similar to that for the day (1.31). The average first day response was 2.11 compared with a second and third day average response of .88. The silent period response averaged .05. In general the crickets responded poorly during the last days of the test. One cricket died on 10 February and the others spent much of their time in the center of the arena around the water vials and food dish. These data did not demonstrate daily periodism in female responsiveness to recorded male calling songs, but the overall level of response was so low that such periodism, if it exists, could have been missed.

The results pointed to the need for further considerations of the physiological readiness of virgin females. Greater response had been noted for other tests of female response. Rather than repeating this test all subsequent testing of virgin female Pictonemobius was in the morning hours corresponding to the first daily peak in male song activity noted in both field and laboratory

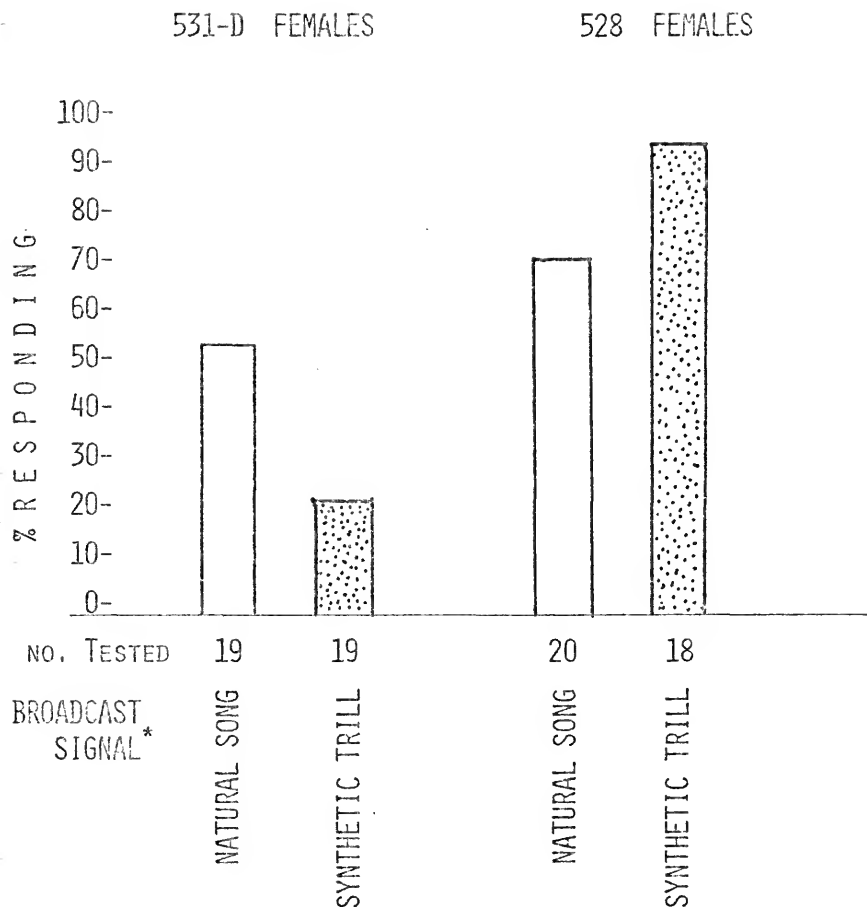
Results

Analysis of Female Response

Square-cut trills, 2 species. When 528 and 531-D laboratory reared virgin females (distinguished from one another by dots of colored paint) were placed together in the arena, it was found they would go to a speaker broadcasting a square-cut, synthetic, continuous trill providing

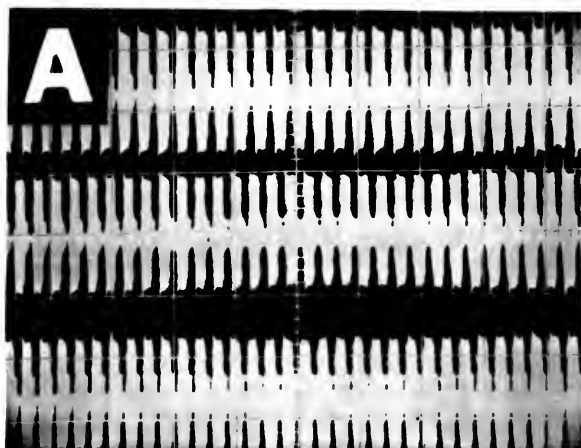
the pulse rate was appropriate. By varying the audio oscillator from the 528 range nr. 36 p/s to the 531-D range nr. 45 p/s, the experimenter could attract 528 in one direction and (by switching speaker and pulse rate) attract 531-D in the opposite direction. No differences could be shown in response by 528 and 531-D virgin females to square-cut, synthetic continuous trills of appropriate pulse rate and their tape-recorded natural calling songs (Fig. 26).

Round-cut trills, 4 species tests. Virgin females of 528, 531-D, 531-B and 525 that were exposed, one species at a time, to a series of seven synthetic round-cut trills each 2.5 p/s apart in the range of their expected response (30.0 to 67.5 p/s). Tape loops of natural calling songs, 38.1, 47.2, 53.8, and 60.4 p/s, respectively, were used as controls throughout. Sixteen different synthetic trills ranging from 30.0 to 67.5 p/s, were used. Portions of three such trills, 30, 32.5, and 35 p/s are shown (Fig. 27). Synthetic trills were used because chirp length varied between the four song types and would likely introduce an additional variable. Each series of seven test signals were presented once each day between 8:00 and 12:00 a.m. EST to a group of 10 crickets of one species. The randomly chosen sequence of presentation began at a different broadcast speaker position each test day enabling each test signal to be broadcast from each speaker once during the three day test period (see previous section for more detailed discussion of methods).

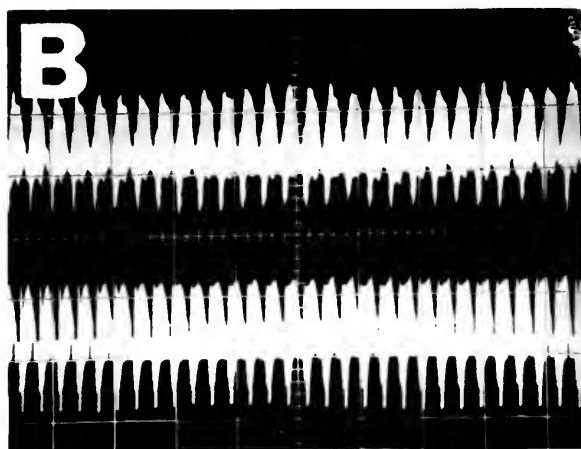


*There was no difference between the broadcast periods and the silent periods at the "dummy" speaker (opposite side of the arena).

Fig. 26. Response to a square cut synthetic trill by virgin female Pictonemobius 528 and 531-D.



SYNTHETIC TRILLS (TOP TO .10 SEC/DIV.
BOTTOM) 30.0, 32.5 AND
35.0 p/s.



NATURAL NEONEMOBIUS .05 SEC/DIV.
CUBENSIS (TOP) WITH
SYNTHETIC PICTONEMOBIUS
525 TRILL, 62.5 p/s
(BOTTOM).

Fig. 27. Oscilloscopic traces of natural (Neonemo-
bius cubensis) and synthetic test signals.

The response to each test broadcast period was evaluated in the following four ways and the data compiled for each method separately. The results show four peaks of female response for each of the four methods corresponding to the calling song pulse rates of each of the four species. Each of the four methods of analysis was an attempt to measure the same test response in different ways.

1. Event recorder counts. As crickets moved to the area in front of a broadcast speaker, they walked onto the sensitive platform (Fig. 18) and triggered the phono-cartridge-sensitive relay system. The number of events or "clicks" of the event recorder pen scribed on a chart for each 6-minute broadcast period was tallied. Unavoidable individual differences between each sensitive platform system with respect to responsiveness to a given cricket movement were averaged out by having each test signal broadcast once at each platform during the three test periods for each species. This tally was compared with the average number of events for the preceding and following 6-minute broadcast of control signal and expressed as a percent of the controls. This was an attempt to reflect the intensity of attraction at the time of each broadcast of test signal and to eliminate the effect of any changes in responsiveness that might have occurred during a test sequence. Female motor activity was the highest during the test and control broadcast periods. The greatest activity occurred when

the test trill pulse rates were in the range of ± 5 p/s of the appropriate male calling song (Fig. 29).

2. Number responding. Any female which turned toward the direction of broadcast sound and moved more than 10 body lengths toward the broadcast speaker with short quick steps characteristic of phonotaxis was given a positive response. The number responding was expressed as a percent of the average number responding during the preceding and following control periods (Fig. 30) (thereby eliminating the effect of different proportions of the females being ready to respond to the pulse rate produced by conspecific males.)

3. Number moving. Movement during each 6-minute experimental period whether silent, test, or control was quantified by totaling the number of individuals moving during the first 2-minute, the second 2-minute and the third 2-minute segments. An index of movement during each test or control period was arrived at by taking the total movement (30 maximum--10 crickets during three, 2-minute periods) and subtracting the total movement (30 maximum) that occurred during the preceding silent period. The purpose of this index was to demonstrate any change in activity that took place during the various test broadcasts. The controls are also plotted to illustrate the crickets' consistent responsiveness throughout the 3-hour test sequence. The results were very similar to the above two methods. The

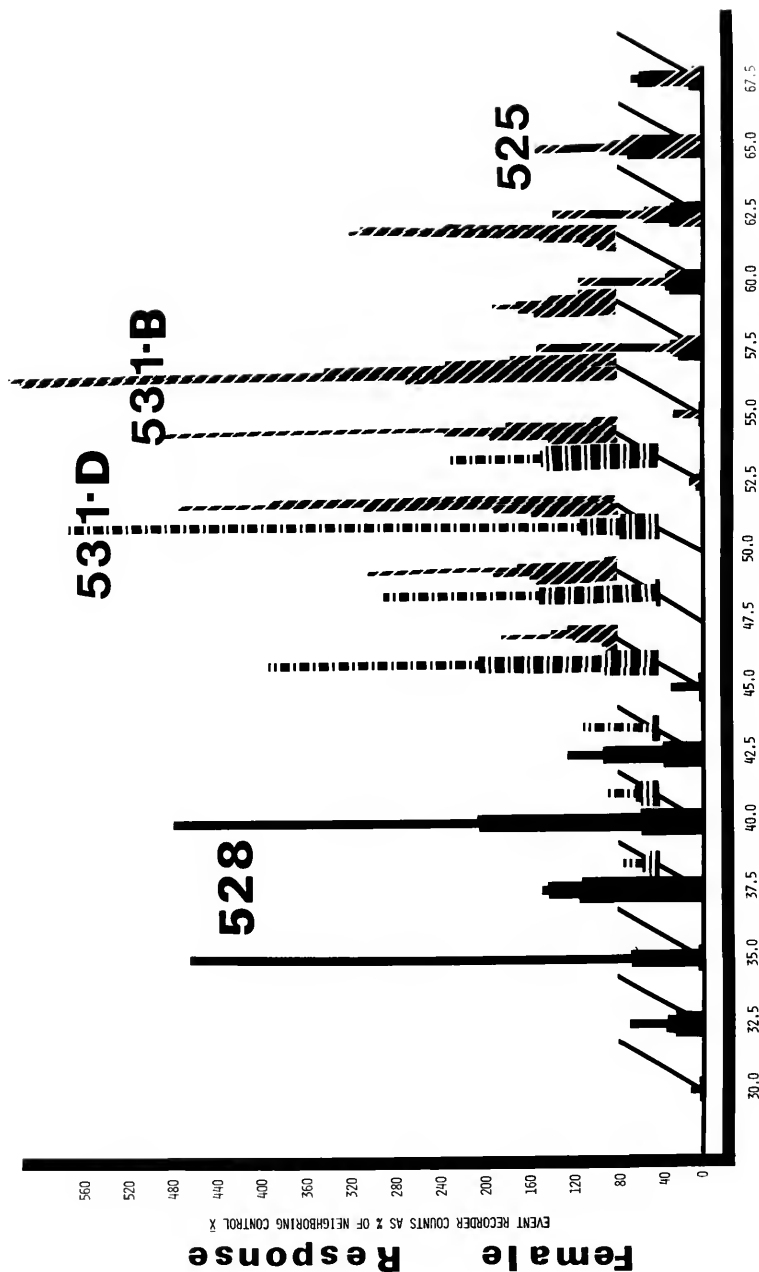


Fig. 29. Female response to pulse rate expressed in event recorder counts as % of neighboring control. Widths of each bar differentiate three component replicates; 6 replicates for 531-B. Bar widths differentiate 3 reps.; 6 reps. for 531-B.

greatest activity occurred in the range of ± 5 p/s of the appropriate calling song for the four species of females tested (Fig. 31).

4. Weighted response index. This measure attempts to score individual females as to how strongly they respond to a given broadcast signal and was done to include a comparison with the event recorder counts. The index was evaluated as the total number of crickets in the "zone of attraction" (less those already present during the preceding 6-minute silent period) of the 0-2-minute period plus 2x the 3-4-minute count plus 3x the 4-6-minute count. Some females climbed the screen directly in front of the speaker and were given 2x the previously outlined values. The sum of all of these is an index of attractiveness shown in Fig. 31 for 528, 531-D, 531-B, and 525. The plot of this index agrees closely with the event recorder counts and describes similar peaks of response, orientation, and activity already described (Fig. 32).

The preceding plots of female response showed a wide range of peak response for each song type tested. This lack of sharp discrimination under these test conditions may have resulted from using females with a low threshold for response in a "single choice" (i.e. no response vs. response to sound) situation. In the field, no female would likely fail for long to be inseminated after becoming responsive to male songs. Hill et al. (1972) found that

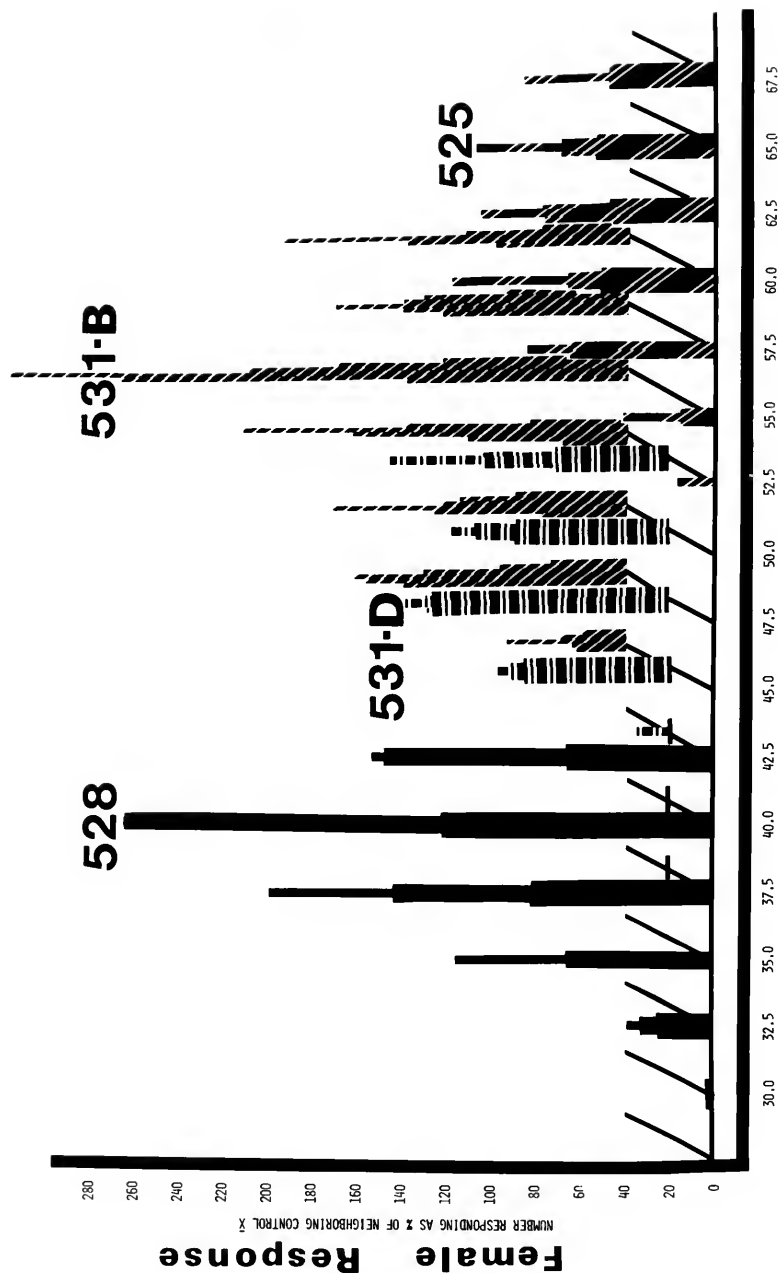


Fig. 30. Female response to pulse rate expressed in numbers responding as % of neighboring control \bar{X} . Bar widths differentiate 3 reps.; 6 reps. for 531-B.

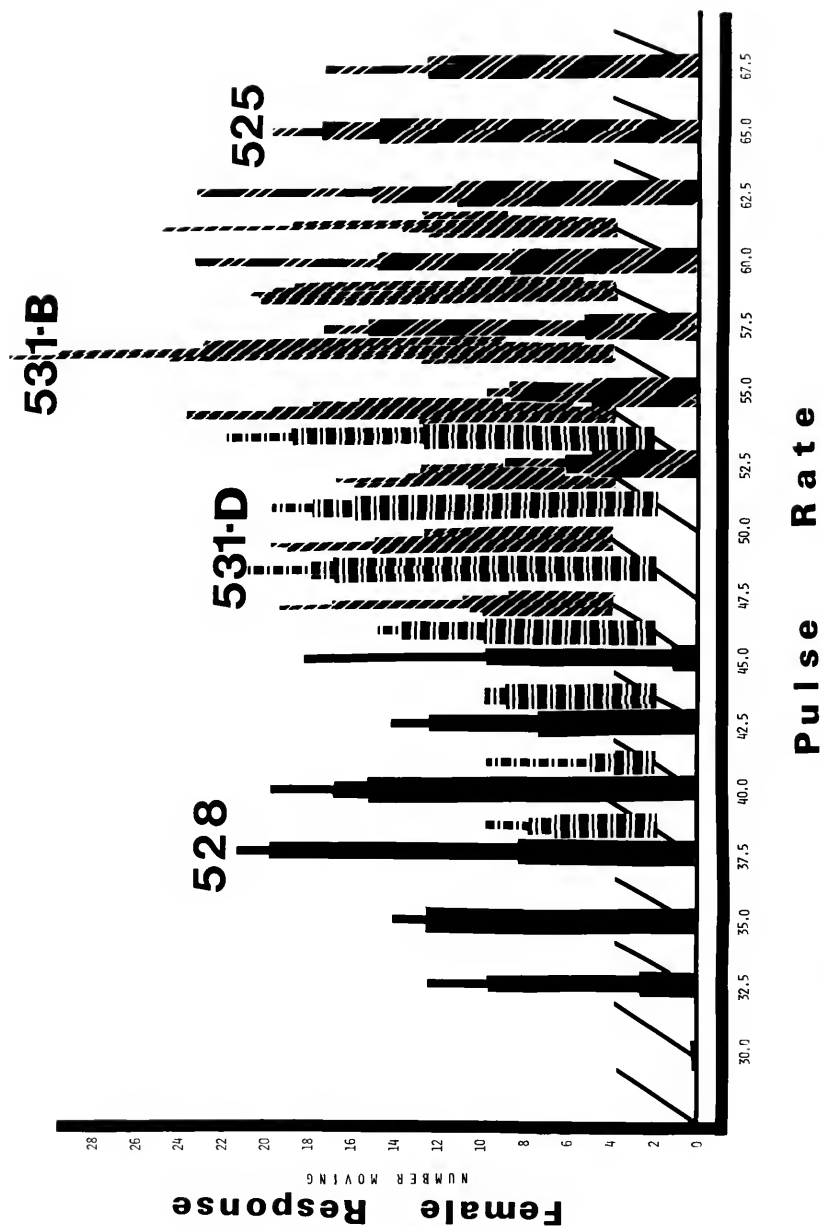


Fig. 31. Female response to pulse rate expressed as number moving. Bar widths differentiate 3 reps.; 6 reps. for 531-B.

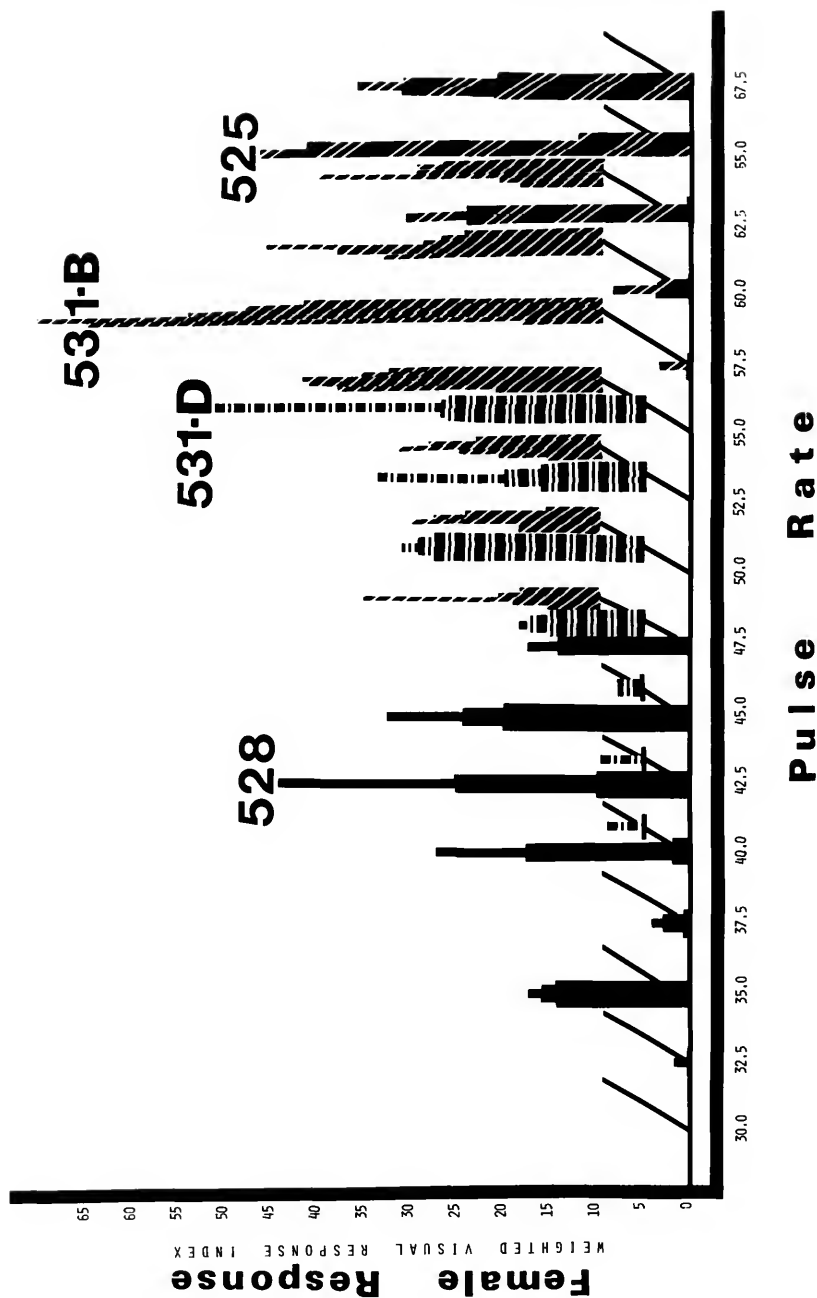


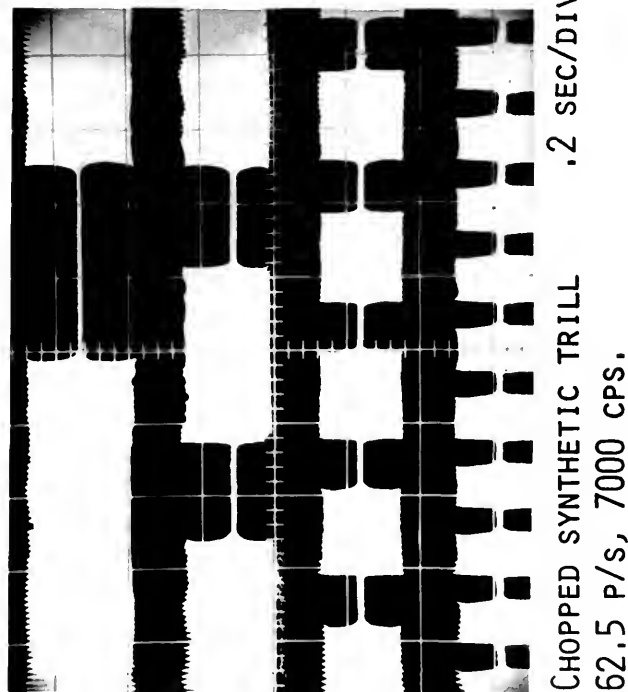
Fig. 32. Female response to pulse rate expressed as weighted visual response index. Bar widths differentiate 3 reps.; 6 reps. for 531-B.

similarly deprived virgin females of Teleogryllus sp. responded in about 50% of the cases to nonconspecific songs. In two choice situations, i.e. no response vs. response to conspecific sound vs. response to nonconspecific sound, Hill et al. (1972) noted that females discriminated nearly 100% of the time.

Artificial trills stimulated the females to greater response than the control calling song, suggesting that continuous trills present an above-normal stimulus, which may have also had the effect of lowering pulse rate discrimination.

Chirp Length

The effect of changing chirp length while maintaining a constant pulse rate and chirp-to-interval ratio, was evaluated using 525 virgin females. Species 525 was chosen because it had the longest chirp of any Pictonemobius and seemed the most likely species to be affected by shortened chirps. Round-cut trills 62.5 p/s (as used in the previous test) were chopped by TG into chirps 4, 8, 16, 32, 64, and 128 pulses long with intervals 1/2 the chirp length, so that each test signal presented the same number of pulses per minute (Fig. 28). Plots of response (Fig. 33) show an increase in response as the chirps approached typical 525 length. Most event recorder and oriented movement counts did not exceed the control average as they did with previous tests on trills, further indicating that a continuous trill provides an above-normal stimulus.



64 PULSES ON - 34 PULSES OFF

32 PULSES ON - 16 PULSES OFF

16 PULSES ON - 8 PULSES OFF

8 PULSES ON - 4 PULSES OFF

Fig. 28. Oscilloscopic traces of a synthetic trill 62.5 p/s chopped into chirps with a chirp-to-interval ratio of 2:1 and a constant number of pulses per minute.

It appears that a chirp of some length is important, yet the short 4-pulse-on, 2-pulse-time-off chirp received some response. When the number of pulses per minute is kept the same, the short pulse-number chirps are too close together and may elicit a response which reflects pulse rate effect rather than a chirp rate effect (Fig. 33).

The calling song of Neonemobius cubensis (Saussure) 537-16, which has a nearly continuous trill similar to that of 525, was added because N. cubensis occurs with 525 in some situations. The N. cubensis test signal (Fig. 27) at 57.1 p/s received the lowest response of all despite its nearly continuous trill close to the 525 pulse rate and being within the range of expected response noted in the pulse rate experiment (Figs. 29, 30, 31, & 32).

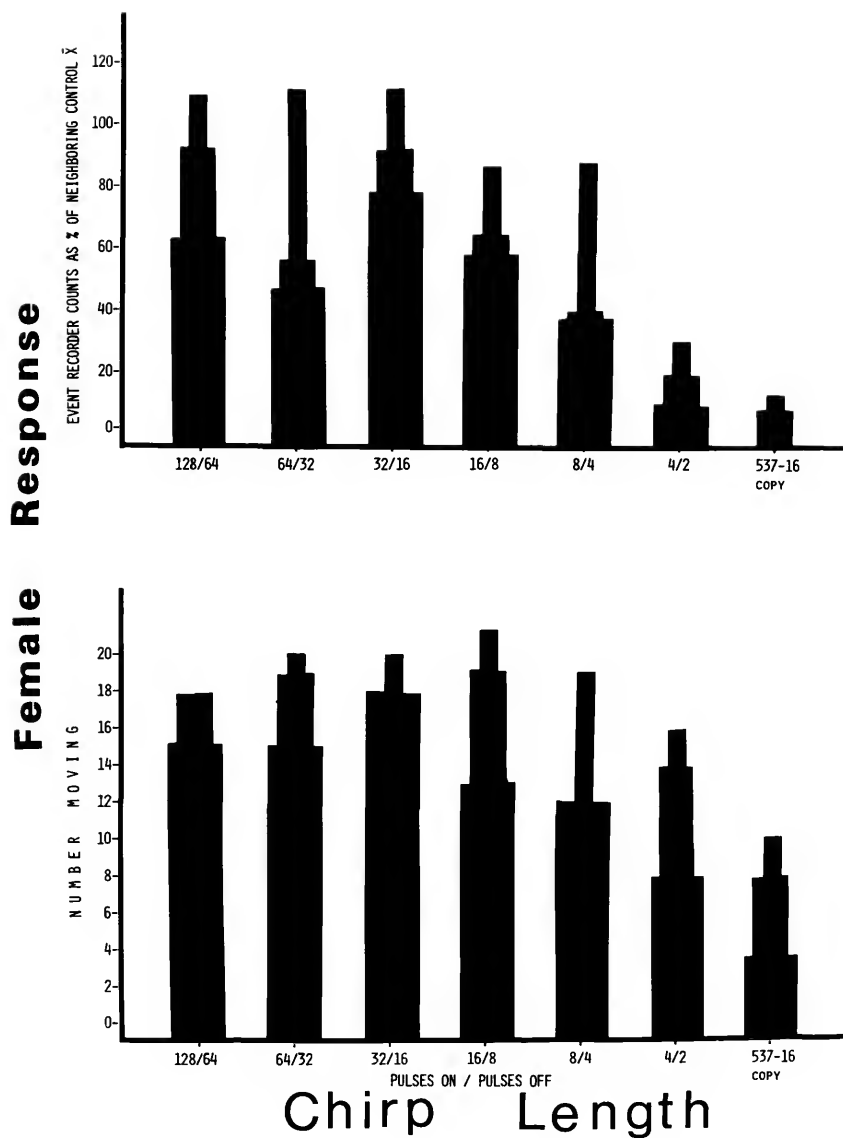


Fig. 33. Effect of chirp length on oriented movement and event recorder counts of *Pictonemobius* sp. 525. Widths of each bar differentiate three component replicates.

HYBRIDIZATION STUDIES

Preliminary Tests

The mating behavior of Pictonemobius (Mays 1971) was studied initially in numerous, small-scale crossing experiments. As techniques improved, larger and more inclusive tests became possible. This section deals with the first replicated tests of Pictonemobius hybridization that I conducted.

Intraspecific Allopatric Crosses

Intraspecific crosses between widely separated populations of what appeared to be the same species of Pictonemobius were successful. In most cases, spermatophores were transferred normally and progeny were produced. No exhaustive series of crosses between distant populations for each of the four song types of Pictonemobius was attempted, but some such crosses were made with the following results: allopatric populations of each song type were interfertile (Table 7).

An Unintentional Interspecific Allopatric Cross

The first Pictonemobius encountered in the vicinity of Gainesville was 531-D and it was assumed to be conspecific with the type of ambitosus. The subsequent discovery of 528 raised the question of which Pictonemobius, (531-D or 528) was the real ambitosus. Two approaches were taken to answer this question. First Dr. T. J. Walker and I went to the vicinity of the type locality described as "Fort Reed -

Table 7. Intraspecific allopatric crosses from selected Florida localities.

Song type	Female locality	Male locality	Normal spermatophore transfer	Progeny
528	N. Levy Co.	Marion Co.	+	*
	Alachua Co.	Marion Co.	+	+
	Marion Co.	Levy Co.	+	*
	Marion Co.	Baker Co.	+	*
	Baker Co.	Alachua Co.	+	+
	Wakulla Co.	Alachua Co.	+	*
531-D	N. Levy Co.	Sumter Co.	+	+
	Marion Co.	Sumter Co.	+	+
	Alachua	Sumter Co.	not seen	+
	Decatur Co. Georgia	Alachua Co.	+	+
531-B	Marion Co. (Dunellon)	Marion Co. (Spaar)	+	+
	Marion Co. (Dunellon)	Levy Co. (Cedar Key)	+	+
	Marion Co. (Dunellon)	N. Palm Beach Co.	+	-
525	Taylor Co.	Alachua Co.	+	+

*No egg hatch perhaps because of dryness. Egg hatch in concurrent laboratory rearing (intraspecific sympatric crosses) was low due to dryness. From this point onward a small portion of the sand in the rearing jar was moistened daily to provide a suitable moisture level for oviposition.

Orange County - 3 mi. S. Mellonville, at the head of navigation on the St. Johns" (Scudder 1877) to collect the "true" ambitosus. "Fort Reed" had been about where the hangar now is at the Sanford Naval Air Station, and on 18 September 1967 we collected Pictonemobius from a nearby area (east 25th Street and Grandview Ave. in Sanford). The specimens collected were brought to Gainesville, reared one generation in the laboratory and crossed with laboratory colonies of 531-D from the Gainesville area to determine if these populations were genetically compatible and could therefore be considered conspecific. The second approach was to borrow from the Museum of Comparative Zoology, Harvard University the (Scudder) type of ambitosus and compare it with 531-D and 528 from Gainesville and the Pictonemobius from near the type locality "Fort Reed."

The results of the cross were unexpected. No progeny were produced in crosses between "Fort Reed" species and Gainesville 531-D (Table 8). However, I subsequently discovered that the 1967 specimens from "Fort Reed" were 531-B and I had unintentionally made an allopatric, inter-specific cross. I identified the type specimen as 531-D; and on the basis of other recent records of 531-D (Fig. 1), I suspect it as well as 531-B still live near "Fort Reed."

Interspecific Sympatric Crosses

Specimens of 528 and 531-D from north Gainesville were crossed to test whether they were genetically compatible.

Table 8. An interspecific allopatric cross between crickets from near the type locality ("Fort Reed," Florida) and crickets (Pictonemobius 531-D) most like the Scudder type of P. ambitiosus.

Female locality	Male locality	Date jar set up*	First Nymphs 1968	# Parents alive 1 May 1968	Nymphs present 28 May, '68
Fort Reed	Alachua Co.	12-15 Feb. '68		2 ♀, 1 ♂	-
Alachua Co.	Fort Reed	12-19 Feb. '68	18 Apr.		+
Alachua Co.	Alachua Co.	12-19 Feb. '68	18 Apr.		+
Alachua Co.	Fort Reed	19 Feb. '68		3 ♂	-

*Test used three males and three females per jar.

Adult females of both species were collected at two sites, the municipal airport and a site 5 miles north on Montecocha Road. The females were placed singly in gallon rearing jars to oviposit. The calling songs of five to ten adult progeny from each parent female were recorded and analyzed for pulse rate, to determine their identity.

Forty-four crosses were set up in gallon jars like those used for the parental females. Only virgin females, obtained by separating nymphal females into separate "sorority" rearing jars, were used. All jars were kept on a 16L:8D photoperiod. Part of the sand in each jar was moistened about every five days. The close spacing of the shelves on which the jars were kept lead to mold formation within the jars. Widening the shelf spacing lead to conditions which appeared to be too dry. This variation in rearing conditions probably caused some loss of egg hatch. Conspecific crosses (528 x 528 and 531-D x 531-D) resulted in progeny in 52.4% of the crosses attempted. Heterospecific crosses (528 x 531-D and 531-D x 528) never resulted in the production of progeny (Table 9).

Another pair of song types, 531-D and 531-B from sympatric populations at 3/4 mi. west of Archer, Florida, were crossed to test whether they were genetically compatible. Individual pairs were observed until a complete mating sequence had elapsed terminating in the female mounting the male with genitalia coupled and spermatophore present. The

Table 9. Interspecific sympatric crosses of Pictonemobius 528 and 531-D, Alachua Co., Fla.

	Control	Control	Control
	528X528 (♀) (♂)	528X531-D (♀) (♂)	531-DX531-D (♀) (♂)
Monteocha Rd.* X	4/4	0/2	0/4
Monteocha Rd.			
Airport** X	0/4	0/4	0/5
Airport			
Monteocha Rd. (♀) X	0/2	0/2	0/1
Airport (♂)			
Airport (♀) X	1/1	0/1	0/2
Monteocha Rd. (♂)			

*Monteocha Rd. = 10 mi. N. Gainesville, west of Fairbanks on SR 225.

**Airport = Gainesville Municipal Airport, NE Gainesville.

males were then removed from the jars and the females were maintained alive for at least 30 days. The results of the crosses are given in Table 10.

Table 10. Interspecific sympatric crosses of Pictonemobius 531-D and 531-B, 3/4 mi. west of Archer, Alachua Co., Florida.

x	Mating Behavior			Progeny Produced
	Premount	Mount	Spermatophore Retained by Female	
531-D x 531-D	+	+	+	+
531-D x 531-B	Mating not seen - pair together for 17 days			-
Jar 1				
Jar 2	+	+		-
531-B x 531-D				
Jar 1	+	+		-
Jar 2	+	+	dropped	-
531-B x 531-B	+	+	+	+

Despite spermatophore transfer (seen for 3 out of 4 test pairs) progeny developed in the control jars only. Test females that received spermatophores from males of song types different from their own did not actively deposit eggs, and appeared similar to unmated virgin females. They repeatedly inserted their ovipositors into the sand but only occasionally were eggs observed in these jars. The abdomens of these test females and those of virgin females became nearly twice

normal size after about 3 weeks. Dissection of such females revealed the ovarioles and oviducts to be filled with 15 to 20 light-brown full-sized eggs with a larger number of white nearly full-sized eggs packed closely behind. These Pictonemobius females from inappropriate matings were similar to the females of Allonemobius (Nemobius) fasciatus of Fulton's 1933 (p. 371) study wherein he found that when the spermatheca was empty "The ovaries were packed with eggs" Lohr and Edson (1973) report that virgin females of Teleogryllus commodus Walker behaved similarly, depositing relatively few eggs and retaining large numbers of eggs in their oviducts. The receipt of some stimulatory factor derived from the testes and transferred by inclusion in the spermatophore, caused oviposition to return to normal levels and fewer eggs to be retained in the oviducts.

Final Test of Hybridization with 4 Species of Pictonemobius

The final study of Pictonemobius hybridization involved crossing each of the four species of Pictonemobius in all 16 possible combinations, and replicating the experiment four times. Before this test was initiated, improvements were made in the selection of test females and in the evaluation of mating sequences.

Methods for Improvement of Mating Tests

To assure the greatest possible success when crossing the four species of Pictonemobius with one another, some

proof of each female's willingness to mate was needed. The effect of age upon a female's willingness to mate was determined by exposing eight virgin laboratory-reared Pictonemobius of each of three species--528, 531-D, and 531-B--to a mature male of their song type for one hour each day. During that time if a mating sequence had proceeded to the stage where the male had produced a spermatophore, the male was removed from the jar and the test scored + for that day. The results of these tests are in Table 11. Three individuals tested on or before their fourth day exhibited no mating behavior. Mating first occurred on the fifth day in two out of four females tested. Mating had occurred by the ninth day in six out of seven females tested. Positive responses were still being recorded on day 43 and later (Table 11). For each of the four song types only virgin females more than seven days old were set aside for further screening prior to testing.

One or two conspecific males were placed in each of several rearing jars containing these age-selected virgin females. When a mating sequence had progressed to where a male with a spermatophore was courting the female, the male was removed from the jar and either used again to determine the readiness of another female or as a test male in the final cross breeding experiment. The female, now considered to be ready to mate, was left alone until the morning of the following day at which time a test male of

Table 11. Age at which virgin females began a mating sequence with mature males.

Species locality	Days after eclosion to adult															
	1-2	3-4	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20	21-22	23-24	25-26	27-28	29-30	31-32
526* Bronson Levy Co.	+	+														
528* Bronson Levy Co.	+	+														
531-B* Romeo Marion Co.	+	+	+		+		+				+					
531-B* Archer Alachua Co.			+	+	+	+	+							+		
531-D** Municipal airport site Alachua Co.				+	+	+										
531-D* Municipal airport site Alachua Co.				+	+			+			+					
528* Municipal airport site Alachua Co.						+	+	+	+	+		+				
528* Municipal airport site Alachua Co.																

- = no spermatophore produced by male (1 hr. test)

+ = spermatophore produced by male (1 hr. test)

Blank spaces indicate no test attempted on these days.

*terminated virgin

**mated on 12th day, terminated

one of the four song types was placed with her for a 4-hour period of observation. This was done for each possible combination of the four different song types (16 crosses) and was replicated four times. The individuals used in this test were from the following localities: (528) .5 mi. east and .5 mi. north of Bronson, Levy Co.: (531-D and 531-B) 3/4 mi. west of Archer, Alachua Co.: (525) .3 mi. east of Clay Co. line on SR.16 and vicinity of Starke Country Club.

The events of Pictonemobius mating (Mays 1971) leading to the production of a spermatophore by the male and its passage to the female were divided into 6 classes to illustrate the degree to which test pairs completed a mating sequence. The test jars were maintained in the laboratory for three months following to determine which crosses resulted in the production of progeny.

Results of Crosses

In the 16 control pairings the mating sequence proceeded normally, although one of these failed to produce progeny. In the remaining 48 heterospecific crosses (Fig. 34) 26 produced calling song; 12 courtship song; 10 the first spermatophoreless mounting; 9 a spermatophore and an attempt at mounting; 4 a spermatophore transfer and its retention by the female for more than 5 minutes; and 1 hybrid progeny with a pulse rate (50.3 n=8) intermediate between the parental types 531-D (47.2 n=9) and 525

		M A L E			
		531-B	531-D	528	525
531-B	1	0	0	0	0
	2	0	0	0	0
	3	0	0	0	0
	4	0	0	0	0
531-D	1	0	0	0	0
	2	0	0	0	0
	3	0	0	0	0
	4	0	0	0	0
528	1	0	0	0	0
	2	0	0	0	0
	3	0	0	0	0
	4	0	0	0	0
525	1	0	0	0	0
	2	0	0	0	0
	3	0	0	0	0
	4	0	0	0	0

LEGEND

* Resulting progeny intermediate pulse rate (50.3, n=8) between 531-D (47.2, n=9) and 525 (59.9, n=8).

blank = no male calling song

0 = calling song

• = courtship song

•• = above plus spermatophorless mounting

••• = above plus spermatophore produced

•••• = above plus mounting and spermatophore insertion

••••• = mounted and feeding on tibial spur, spermatophore remains on female minimum 5 minutes.

XXXXXX = progeny present in jars during following three months.

Fig. 34. Mating behavior and progeny production in crosses of Pictonemobius 528, 531-D, 531-B, and 525.

(59.9 $n=8$). All other reported interspecific crosses between crickets have resulted in intermediate songs (Alexander 1968).

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APPENDIX A

The Use of Stridulatory File Characteristics in Identification of Pictonemobius

The stridulatory files of more than 150 Pictonemobius from 7 sites of sympatry were measured, and the number of teeth counted (Table 1, Appendix). Tape recorded specimens were used whenever possible. In general, 528 and 531-D had the longest files. For all of the Pictonemobius examined, the longer files tended to have more teeth. The use of stridulatory file characteristics can sometimes be of assistance in identification of Pictonemobius.

Appendix Table 1. Characteristic of stridulatory files of four species of Pictonemobius.

Song type & locality	n	No. of teeth		Length of file (mm)		Teeth/mm	
		Mean-SD	Range	Mean-SD	Range	Mean-SD	Range
<u>Pictonemobius 531-B</u>							
Seminole Co. near "Fort Reed," Sanford	5	88.8 \pm 6	81-97	0.77 \pm .05	0.69-0.82	115 \pm 3	112-118
Alachua Co., 3/4 mi. west of Archer	15	85.0 \pm 5	79-94	0.84 \pm .04	0.76 \pm 0.92	101 \pm 5	94-108
Levy Co., Bronson	6	87.7 \pm 5	79-91	0.85 \pm .05	0.77-0.89	103 \pm 2	100-107
Collier Co.	4	93.2 \pm 4	88-97	0.82 \pm .06	0.76-0.89	114 \pm 4	110-118
Taylor Co. Blue Springs	5	96.4 \pm 5	88-102	0.94 \pm .04	0.89-1.00	102 \pm 9	94-113
Palm Beach Co. Jupiter	6	84.3 \pm 6	78-90	0.73 \pm .04	0.69-0.77	117 \pm 3	113-119
<u>Pictonemobius 525</u>							
Alachua Co. S200A & 301	15	82.7 \pm 4	75-90	0.89 \pm .05	0.79-0.94	93 \pm 4	86-101
Taylor Co. Perry & 5 mi. S. Perry	3	89.0 \pm 8	80-96	0.86 \pm .07	0.79-0.92	104 \pm 6	99-111
Walton Co., nr. Ebro	2	85.0 \pm 3	83-87	0.81 \pm .07	0.76-0.86	106 \pm 13	96-115

Appendix Table 1 - continued

Song type & locality	n	No. of teeth		Length of file (mm)		Teeth/mm	
		Mean-SD	Range	Mean-SD	Range	Mean-SD	Range
<u>Pictonemobius 528</u>							
Taylor Co. Perry, Fla.	2	106.5+5	103-110	1.00+-.01	0.99-1.00	107+4	104-110
Levy Co. Bronson	16	101.6+7	100-124	1.00+-.05	0.93-1.08	108+6	98-121
Baker	7	109.4+9	94-119	1.00+-.06	0.91-1.08	100+7	97-117
Franklin Co. Carrabelle nr. Gainesville	5	97.4+2	95-100	0.91+-.04	0.85+0.96	107+3	104-111
Alachua Co. Field coll. Several localities	13	117.5+6	108+127	1.02+-.07	0.92-1.16	116+6	106-127
Lab reared One locality	10	114.7+7	105-124	1.03+-.05	0.94-1.14	111+7	101-123
Clay Co., Fla. nr. Goldhead Branch St. pk.	10	92.4+4	84-100	1.07+-.05	1.01-1.14	86+5	82-96
<u>Pictonemobius 531-DqX525d</u>							
Hybrid Test #69 Lab Reared	4	85.5+6	78-92	0.85+-.08	0.78-0.93	101+7	93-111

Appendix Table 1 - continued

Song type & locality	n	No. of teeth		Length of file (mm)		Teeth/mm	
		Mean-SD	Range	Mean-SD	Range	Mean-SD	Range
<u>Pictonemobius ambitiosus (531-D)</u>							
Alachua Co., 3/4 mi. west of Archer	8	109.4+6	101-120	0.97+ <u>0.06</u>	0.89-1.08	113+6	101-120
Levy Co., Manatee Spr.	5	104.0+10	92-119	0.96+ <u>0.05</u>	0.89+1.04	108+9	98-120
Levy Co., 1 mi. N. Bronson	4	93.8+1	92-95	0.89+ <u>0.05</u>	0.82+0.91	106+4	103-112
Alachua Co., nr. Gainesville	14	105.9+9	93-125	0.94+ <u>0.07</u>	0.83-1.07	113+9	94+127 [#]
Clay Co. (Goldhead Branch St. Pk.)	10	99.4+6	91-109	0.84+ <u>0.07</u>	0.80-0.99	113+6	103-122
Seminole Co. "Fort Reed" nr. Sanford. Type of Nemobius ambitiosus	1	115		0.98		117	

APPENDIX B

A Key to the Adults of *Pictonemobius*

The following key should provide the user with a greater than 90% chance of identifying a pinned specimen of the genus *Pictonemobius* to species, providing locality and habitat information are available and color pattern (especially of females) is not altered by poor preservation techniques. The distribution maps (Figs. 3, 4, 5, & 6) will aid in the use of this key.

Specimens from west of Lafayette and Dixie counties in the panhandle region of Florida are difficult to classify in terms of color pattern and song (Table 1, 525). This area is ecologically different from the rest of Florida where *Pictonemobius* occurs. Such a region could contain a fifth *Pictonemobius* or may represent a zone of introgression where two or more of the species defined for peninsular Florida are united.

The status of these populations can only be ascertained by further studies.

A Key to Adults of Pictonemobius

- 1a. Male tegmina with distinct yellow or cream-colored border; female tegmina with light-colored dorso-lateral stripe and dorsal field usually speckled or flecked; occurring in mesic to xeric habitats over most of Florida. 2
- 2a. Female tegmina dark ground color; entire lateral stripe bright* at least 1/4 as wide as tegmina, epiproct white (living specimens); males, pronotum lighter than wings, often purplish; metathoracic femora uniform buff to orange brown, lighter than pronotum, striping or marking absent or nearly absent* [*Collier County - tegmina (female) lighter, stripe less distinct; metathoracic femora more strongly spotted and striped]. . Pictonemobius 531-B
- 2b. Female tegmina color tan to black with white and brown spots; lateral stripe diminishing in color and width distally less than 1/4 as wide as tegmina, epiproct not white; male pronotum usually darker than wings, metathoracic femora bicolored, striped and dark spotted on white to nearly dark brown ground color. 3
- 3a. Female tegmina usually brown with a central dark spot proximally and faint light specks overall, lateral stripe indistinct beyond humeral angle; female abdomen concolorous with

tegmina, no distinct lateral striping; general body color of both sexes brown, lacking contrasting patterning or speckling.
 Pictonemobius 531-D

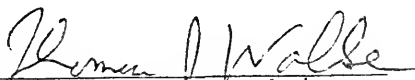
3b. Female tegmina usually charcoal, with numerous light brown to white speckled areas; lateral stripe extending beyond humeral angle; female abdomen with dorsal black central stripe darker than tegmina, 1/3 width of abdomen bordered by white speckled to brown dorso-lateral areas; general body color of both sexes black with white speckling overall. . . Pictonemobius 528

1b. Male tegmina without distinct border; female tegmina without dorso-lateral stripe and with dorsal field usually uniform dense flat chocolate brown or black; occurring in pine flatwoods in northeast Florida, and from flatwoods and river bottom land to the pine forests in the northwest and the panhandle of Florida.* [*northwest and panhandle Florida individuals are lighter in overall coloration, resembling 531-D].

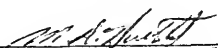
Biographical Sketch

David Lee Mays was born 22 May 1941 in Santa Monica, California. His interests in insects began when he was 10 years of age. With generous parental encouragement he developed a collection of more than 15,000 insect specimens by the time he entered University High School in West Los Angeles. He attended Santa Monica City College in early 1960 and transferred to Oregon State University later that fall to enter the School of Forestry. Upon learning of the staff and facilities of the Department of Entomology at Corvallis he instead entered the School of Science and received the degree of Bachelor of Science in entomology in 1964, and the degree of Master of Science in entomology with a minor in genetics in 1966. From that time to present date he has worked toward the Doctor of Philosophy degree in the Department of Entomology and Nematology at the University of Florida.

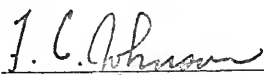
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


Thomas J. Walker, Chairman
Professor of Entomology
and Nematology

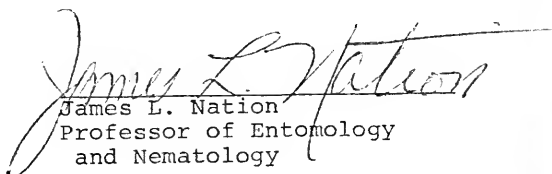
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


Milton D. Huettel
Assistant Professor of
Entomology and Nematology


I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


F. C. Johnson
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


James L. Nation
Professor of Entomology
and Nematology

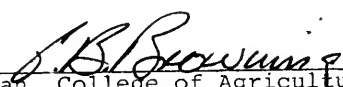
I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



S. H. Kerr
Professor of Entomology
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